Late Quaternary faunal responses to environmental change and isolation on a large Australian land-bridge island

by

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Doctor of Philosophy

To my wife and friend,

Linda-Marie

“*Modification of form is admitted to be a matter of time. The amount of diversity in the organic remains of two beds or strata is a measure of the time between the deposition of those strata. So the amount of diversity in the species of two adjacent islands is the measure of the time those islands have been separated.*”

Alfred Russel Wallace (1864 p. 111).

Wallace, A. R. (1864). Remarks on the habits, distribution, and affinities of the genus *Pitta*. *Ibis* **6**, 100–114.

CONTENTS

ABSTRACT

Islands have been a focus for the study of evolutionary and ecological processes since the time of Darwin and Wallace. In this study I examine faunal responses to climate change and isolation on Kangaroo Island (KI), South Australia, over approximately the last 50 thousand years (kyr). KI lies off the south coast of South Australia near the edge of the continental-shelf. It retains the largest proportion (47%) of uncleared natural vegetation in any of the agricultural districts of southern Australia and has been spared the introduction of rabbits and foxes. In addition, it is the only part of Australia that was not inhabited by Aboriginals at the time of European colonisation. Consequently, KI may retain the best-preserved natural ecology in southern Australia and is therefore vital for the conservation of southern Australia's biodiversity.

Prior to isolation, land-bridge islands typically support diverse 'mainland' faunas that, once isolated, suffer elevated selection pressures and extinction rates. Therefore, island fossil records can provide detailed archives of how faunas responded to past environmental change and isolation and offer excellent potential analogues for predicting the long-term impacts of anthropogenic habitat fragmentation. KI was isolated from the mainland by rising sea-levels around 9 kyr ago. Here I examine variations in stable isotopes, sedimentology, geochemistry, chronology and non-volant mammalian fauna from a Late Pleistocene–Holocene fossil assemblage excavated from Kelly Hill Cave (KHC; CEGSA No. 5K1) in the Kelly Hill Caves complex. KI's existing Late Pleistocene–Holocene fossil mammal assemblages are re-examined and pre-European faunas of Eyre and Yorke Peninsulas are also investigated.

The KHC fossil assemblage spans from >20 to 7 kyr ago and records shifts in mammal community composition across the Last Glacial Maximum (LGM) and Holocene isolation. Total species richness did not vary greatly through the sequence, but relative abundances of ecologically divergent species varied greatly. Several heath species were abundant during the relatively cool, dry Late Pleistocene but declined with the onset of relatively warmer, wetter Holocene conditions. Arid zone species were most abundant during the LGM only and mallee/woodland species became more abundant during the Holocene. These patterns are supported by stable isotope and sedimentary records. The mammals excavated from KHC clearly responded to climate change, but only three species were extirpated from the sequence during the LGM. This bolsters an emerging view that Australia’s native fauna was highly resilient to climate change. A further four species disappear within 2 kyr of KI’s isolation, but all were previously rare. Nineteen species were extirpated from KI between 7 kyr ago and the Present, many of which were lost soon after isolation, which is consistent with the predictions of island biogeographic theory. As the fossil record between 7 kyr and Present is provided by nearby archaeological assemblages that doubtless have different collection biases, locating and analysing fossil deposits younger than 7 kyr will be an important focus of future studies.

DECLARATION

I certify that this thesis does not incorporate without acknowledgment any material previously submitted for a degree or diploma in any university; and that to the best of my knowledge and belief it does not contain any material previously published or written by another person except where due reference is made in the text.

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Matthew McDowell

21 February 2013

PREFACE

Chapters 2–7 are either published papers or manuscripts intended for publication in scientific journals as stand-alone pieces of work. Consequently, some repetition was unavoidable. In addition, there are some differences in style between chapters due to the requirements of the targeted journal. However, all cited references appear in the bibliography at the end of this thesis in consistant format. The reference style of unpublished manuscripts follows the Harvard system format.

The intellectual development and writing of this thesis was carried out by the author. Co-authors are included on papers or manuscripts to acknowledge their contribution of significant background information, discussion and/or editorial comments.

LIST OF PUBLISHED PAPERS AND MANUSCRIPTS

Paper 1. McDowell, M. C., Prideaux, G. J. and Walshe, K. E. (in preparation). Re-evaluating the Late Quaternary mammal fossil assemblage of Seton Rockshelter, Kangaroo Island, South Australia, including the evidence for late-surviving megafauna.

Paper 2. McDowell, M. C., Prideaux, G. J. and Baynes, A. (in preparation). The taxonomic resurrection of *Bettongia anhydra* (Marsupialia: Macropodidae).

Paper 3. McDowell, M. C. and Medlin, G. C. (2010). Natural Resource Management implications of the pre-European non-volant mammal fauna of the southern tip of Eyre Peninsula, South Australia. *Australian Mammalogy* **32**, 87–93.

Paper 4. McDowell, M. C., Baynes, A., Medlin, G. C. and Prideaux, G. J. (2012). The impact of European colonization on the late-Holocene non-volant mammals of Yorke Peninsula, South Australia. *The Holocene* **22**, 1441–1450.

Paper 5. McDowell, M. C., Bestland, E. A. Bertuch, F. Ayliffe, L. K., Hellstrom, J. C., Jacobsen, G. E. and Prideaux, G. J. (2013). Chronology, stratigraphy and palaeoenvironmental interpretation of a Late Pleistocene to mid-Holocene cave accumulation on Kangaroo Island, South Australia. *Boreas* in press (accepted 8-Feb-2013).

Paper 6. McDowell, M. C., Prideaux, G. J., Baynes, A., Ayliffe, L. K., Bertuch, F., Hellstrom, J. C. and Jacobsen, G. E. (in preparation). Late Quaternary faunal responses to isolation and environmental change on a large Australian land-bridge island.

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CHAPTER 1

General Introduction

Description of research problem

Islands have been a focus for the study of evolutionary and ecological processes since the time of Darwin and Wallace (e. g., Darwin 1859; Wallace 1895), offering “valuable insights into speciation and adaptive radiation, and the importance of contingency and determinism in evolutionary diversification” (Losos and Rickleffs 2009 p. 830). The overall objective of this study is to examine faunal responses to environmental change and isolation on Kangaroo Island (KI), South Australia, over the last 40 thousand years (kyr). In contrast to oceanic islands which are perpetually isolated KI is a land-bridge or continental-shelf island. Land-bridge islands are high points on continental shelves that are isolated from the adjacent mainland during warm climatic phases when sea levels are high, but connect with the mainland during cold phases when sea-levels are much lower (Whittaker and Fernández-Palacios 1998). Most islands are small and have distinct boundaries, lower species diversity and limited immigration potential. Consequently, environmental changes have a strong influence due to factors including rainfall and sea level fluctuations, reduced genetic diversity and low potential for moving to different habitats (e. g., Lister 1995; Mills *et al*. 2004; Jones Lennon *et al*. 2011; Miller *et al*. 2011).

Islands can provide refugia for species whose mainland populations have been decimated by habitat loss, competition with and/or predation by exotic species (e. g., Vartanyan *et al*. 1993; Lister 2004; van der Geer 2010). However, island populations also frequently experience reduced genetic diversity making them more susceptible to extirpation and extinction (Kadmon and Pulliam 1993; Johnson *et al*. 2000; Brown *et al*. 2001; Magurran and Henderson 2003; Mills *et al*. 2004). Unlike mainland populations which can migrate with their ecological niche as it shifts due to climate change, species isolated on islands must adapt or be extirpated. As a result, organisms isolated on islands tend to evolve differently and more rapidly than their mainland equivalents (MacArthur and Wilson 1963, 1967; Adler and Levins 1994; Berry 1996; Lomolino 2005; Raia and Meiri 2006).

There are several examples of present-day species that have been extirpated from their mainland range and persist only on islands e. g., *Bettongia lesueur* (Short and Turner 2000), *Perameles bougainville* (Short *et al*. 1998), *Lagostrophus fasciatus* (Helgen and Flannery 2003) *Leporillus conditor* (Copley 1999) and *Sminthopsis aitkeni* (Gates 2001). In addition, Turney *et al*. (2008) reported that several species of megafauna survived on Tasmania up to 6 kyr after they became extinct on mainland Australia. Islands are therefore of enormous conservation importance for Australian native mammals (e. g., Burbidge *et al*. 1997; Burbidge and Manly 2002). Consequently, it is vital that we understand how island-bound mammals responded to environmental change and isolation in the past. Land-bridge islands are of particular interest because when initially isolated they support high-diversity mainland communities that suffer elevated selection pressures and extinction rates, making them excellent potential analogues for assessing the long-term effects of anthropogenic habitat fragmentation.

MacArthur and Wilson (1967) revolutionised the study of island faunas with their equilibrium theory of island biogeography which provided a rigid framework for studying diversity and distribution of species on islands. Many researchers have since examined the influence of island size, dispersal distances, competitors and predators, and habitat structure on island species and communities. Most research centred on oceanic islands, which have impoverished faunas biased toward species with water-crossing abilities. By contrast, land-bridge islands are initially supersaturated after isolation, supporting a species-rich continental fauna rather than a lower number of species typical of oceanic islands and predicted by equilibrium theory (Diamond 1972; Wilcox 1978). As the fauna "relaxes" extirpation rates exceed those on oceanic islands and are inversely proportional to island size (Diamond 1975). The theory of island biogeography has since been applied to numerous isolated habitat "islands" such as desert-bound montane forest, mountain tops, reserves and artificial islands created by reservoir inundation (Kadmon and Pulliam 1993; Cosson *et al*. 1999; Terborgh *et al*. 2001; Lambert *et al*. 2003). All follow a similar pathway of extirpation trailing in the wake of isolation by Quaternary climatic fluctuations (Brown 1971; Lomolino *et al*. 1989) or human landscape modification (Newmark 1987; Laurance 1991; Foufopoulos *et al*. 2011).

Past land-bridge island research focussed on short-term studies after recent fragmentation which can only track initial adjustment (Kadmon and Pulliam 1993; Cosson *et al*. 1999; Foufopoulos and Ives 1999; Terborgh *et al*. 2001; Lambert *et al*. 2003) and studies examining climatically driven processes over thousands of years. To date long-term studies have only shown or predicted what species lived on islands at some point in the past compared to what inhabits them now.

KI was chosen as the study area because it is the only land-bridge island on Earth known to have near complete vertebrate, vegetative and associated environmental records spanning not only the last 10 kyr but most of the Late Quaternary. It is Australia's third largest land-bridge island (4,405 km^2) and is geologically continuous with the adjacent Fleurieu Peninsula. In addition, the western part of KI shares a thin surface veneer of Bridgewater Formation (Pleistocene aeolian calcarenite) with the Eyre and Yorke Peninsulas (Belperio and Flint 1999). These regions likely supported similar mammal faunas before rising sea-level isolated KI 8.9 kyr ago (Hope *et al*. 1977; Belperio and Flint 1999). This event, the primary focus of this study, was the last of a series of separations that occurred three times in the Late Quaternary and multiple times during warmer phases of the Pleistocene (Belperio 1995).

KI retains the most native vegetation of any southern Australian agricultural district (47%), but perhaps more importantly, is free of wild rabbits and foxes (Robinson and Armstrong 1999). It is therefore of paramount conservation and economic importance. KI was the only region of Australia not inhabited by Aborigines when Europeans arrived, although archaeological evidence reveals KI was occupied from at least 16 kyr ago to around 5 kyr ago (Hope *et al*. 1977; Robinson and Armstrong 1999). This study is unique because in it I examine how fauna actually responded to the effects of island isolation using palaeontological data. This project will set a new benchmark in our understanding of island ecosystems and will have important implications in light of modern climate change and anthropogenic habitat disturbances.

Objectives of the study

The primary objective of this study was to gain a better understanding of the effects that climate change and isolation had on non-volant Australian mammals, information that is crucial to their conservation and protection. It also provides excellent potential analogues for assessing the long-term effects of anthropogenic habitat fragmentation. Several Late Pleistocene and Holocene fossil assemblages are known from KI, but most are neither temporally well-defined nor span long periods of continuous deposition. The primary study site is located in the Kelly Hill Caves complex. The excavation site was selected based on the presence of fossil bones on and in surface sediments, likelihood of stratigraphic integrity and likelihood of minimal disturbance, depth of sediment and presence of speleothem growth above the excavation site (indicating potential speleothem growth in the sediment). Secondary sites on KI and Eyre and Yorke Peninsulas were also investigated to allow comparison with faunas that experienced a smaller degree of isolation.

Aims

The aims of this thesis are to:

1. Determine the effects that Late Pleistocene climate change had on the fauna of KI, which was still part of the mainland at that time;
2. Determine the effects that isolation had on the fauna of KI;
3. Assess the potential for late-surviving megafauna on KI.
4. Test the predictions of the equilibrium theory of island biogeography (MacArthur and Wilson 1967) using palaeontological data that indicate how fauna actually responded to the effects of island isolation;
5. Provide potential analogues for predicting the long-term impacts of anthropogenic habitat fragmentation;
6. Provide baseline information to conservation, natural resource and landscape managers.

Research progression

This thesis is structured to provide a clear and coherent guide to the research progression. It is presented in manuscript/published paper format to allow submission of publication with minimal alteration. Each chapter investigates a different aspect of the research problem. The collection from Seton Rockshelter, the only previously excavated KI accumulation covering the time-period of interest, was reanalysed. The chronology, stratigraphy, geochemical and physical characteristics of KHC's stratigraphy were assessed and interpreted. Changes in fauna and stable isotopes obtained from land-snails were assessed and correlated with known climate change and sea-level fluctuations. The taxonomy of genus *Bettongia* was investigated to determine which species occurred on KI, which lead to the recognition of *Bettongia anhydra* as a distinct species. Finally, the pre-European faunas of southern Eyre and Yorke Peninsulas, considered pseudo-islands, were assessed then compared with the fauna of KI in the General Discussion to investigate the effects of different degrees of isolation.

LITERATURE REVIEW

Palaeoecology

Over the last 200 years Australia has seen the highest rate of mammalian extinction anywhere in the world (Morton 1990; Letnic 2000), largely due to environmental change resulting from extensive grazing by introduced feral and domestic livestock and pressure from introduced predators (Burbidge and McKenzie 1989; Morton 1990, 1995; Pickup and Stafford Smith 1993). Environmental change poses direct and indirect challenges to all living organisms, affecting the availability of food and shelter, which influences an organism's distribution and abundance and ultimately their ability to survive in a given environment. Consequently, environmental change has had serious impacts on global biodiversity (Morton 1990; Hadly 1996; Bowman 2001; Scholes and Biggs 2005; Millar and Brubaker 2006). However, it is also considered one of the driving forces of speciation (Barnosky 2005). Biodiversity has become increasingly used as a tool to measure ecosystem health, and is also being used in the formulation of natural resource management (NRM) policy and practice for the prevention of habitat loss and species extinction (Department for Environment and Heritage 2007). In addition, Barnosky and Shabel (2005) suggested that species richness and biodiversity may be useful tools for assessing community perturbation against a long-term baseline.

Faced with environmental change, organisms may remain unaffected, or may respond with dispersal, population size or density change, clinal shift, evolution, extirpation or extinction (Hadly 1996; Barnosky and Bell 2003; Barnosky 2008). It is therefore of fundamental conservation, agricultural and economic importance that we understand the impact of environmental change as a key to predicting and preparing for future changes in biodiversity. Such predictions rely on a detailed understanding of the impacts of past environmental variation, yet few data sets used in biodiversity assessments span more than one full generation of the targeted organism (Willis *et al.* 2005; Willis *et al*. 2007; Froyd and Willis 2008). When historical records do not provide adequate temporal depth, natural resource and land managers can turn to the study of Quaternary palaeoecology to develop a better understand of the ecology of extant organisms and their response to previous environmental change (Birks 1996; Lyman 1996; Delcourt and Delcourt 1998; Swetnam *et al*. 1999; Jackson and Erwin 2006; Froyd and Willis 2008).

Many authors (e. g., Andrews 1990; Behrensmeyer 1991; Graham 1993) argued that post-mortem, pre-discovery processes can bias the fossil record, making it impossible to estimate a species presence/absence and population size because:

1. Animal remains may not be preserved in a fossil assemblage (a taphonomic issue);
2. The small proportion of animal remains that are preserved may not be found by palaeontologists (a taphonomic issue);
3. Remains that are preserved and found may not be collected (a recovery issue);
4. Remains that are preserved and found may not be sampled (a sampling issue);
5. Remains that are recovered may not be identifiable to a taxonomic level of interest.

These considerations vary between different taxa, different skeletal elements of each taxon and between deposits (Grayson 1984; Lyman 1994, 2008). Ultimately we can never (in an empirically testable way) analytically estimate with a known level of accuracy the living population on the landscape that fossil remains represent. However, studies that estimate how accurately recent animal accumulations reflect the living fauna from which they were sampled indicate that we *can* accurately estimate the relative abundances of taxa in a community (e. g., Avenant 2005; Western and Behrensmeyer 2009; Terry 2010a, b; Miller 2011). Based on such studies, we can assume that the abundances of osteological remains in a fossil assemblage probably reflect their relative abundances in a palaeocommunity allowing us to analytically monitor general trends in relative taxonomic abundances in an area over time (Lyman 2012a, b).

Fossil assemblages may also be biased by 'time-averaging'. This mixing of different aged fossils may skew relative abundances and inhibit palaeoecological interpretation. However, some researchers (e. g., Kidwell and Flessa 1995; Hadly 1999; Barnosky and Shabel 2005; Millar and Brubaker 2006) showed that fossil assemblages can provide an accurate record of the palaeocommunity sampled. Some researchers (Hadly 1999; Barnosky *et al*. 2003; Barnosky and Shabel 2005) have even posited that, due to the inclusion of rare taxa, a degree of time-averaging can be beneficial for the interpretation of both present and past ecosystems. Regardless, the type and degree of taphonomic bias, including agents of accumulation and burial processes, must be considered when interpreting palaeocommunities (Lyman 1994). Each agent of accumulation (e. g., pitfall trap, mammalian predator or avian predator) samples the living palaeocommunity in a different but predominantly consistent pattern, biasing the accumulation of their prey in a certain way (Douglas *et al*. 1966; Lundelius 1966; Dodson and Wexlar 1979; Kusmer 1990; Baird 1991; Walshe 2000; Reed 2006). In many cases these accumulation characteristics can be used to identify the agent responsible for the accumulation, allowing the researcher to compensate for the bias and better interpret the palaeocommunity (see Appendix 1).

Palaeontological records provide one of the few reliable sources of knowledge regarding the past distribution and relative abundance of Australia’s fauna (McDowell 1997; Jackson and Erwin 2006; Lyman 2012b). When combined with reliable chronology (see Appendix 2) that demonstrates temporal continuity, fossil assemblages can be analysed to reconstruct past environmental conditions that can be applied to specific ecological and environmental questions (Birks 1996; Millar and Brubaker 2006). In addition, palaeoecological records can be used to investigate biodiversity maintenance, the naturalness of an ecosystem, conservation evaluations, habitat modifications, changes in disturbance regimes, re-colonisation and invasions (Birks 1996; Lyman 2006; Willis and Birks 2006). Because Quaternary vertebrate fossil localities are quite common and contain many extant taxa, they are particularly important as sources of data for global change and palaeoecological research (Foster *et al.*1990; Gajewski 1993; Delcourt and Delcourt 1998; Hadly 1999).

Three important metrics that are used by neo-ecologists to monitor ecosystems can be easily applied to palaeoecology. 1, species richness (how many species there are). 2, species composition (what species are there) and 3, species relative abundance (how common or rare individuals of a species are relevant to each other) (Jablonski and Sepkoski 1996; Hadly and Barnosky 2009).

The presence of a given species is indicative of the presence of a given ecological niche, and the persistence of a that species is indicative of the persistence of that ecological niche. Therefore, assuming uniformitarianism, the species composition of a palaeo-community can be used to interpret the palaeo-ecosystem (Jackson and Erwin 2006; Hadly and Barnosky 2009). This can be used to inform neo-ecologists about which species “should” be present in a given ecosystem (in the absence of human manipulation), whether the loss or gain of a given species is unusual, and whether the normal number of species that an ecosystem could be expected to support are actually present (Hadly and Barnosky 2009).

The abundance of a species is related to its life history attributes (e. g., body size, generation period, habitat preference etc.) as well as the abundance of habitat within an ecosystem that can support individuals of a given species (Blois and Hadly 2009). Pronounced changes in the relative abundance of species can indicate change in landscape characteristics (for example, expansion of xeric microhabitats at the expense of mesic ones) and may indicate major shifts in species interaction (e. g., reducing the relative abundance of predators could increase the relative abundance of herbivores). Monitoring species richness is critical because it correlates with ecosystem attributes such as productivity, habitat disturbance, and habitat heterogeneity (Hadly and Barnosky 2009). Thus, dramatic changes in richness may indicate fundamental changes in an ecosystem or may relate to sample size (Hammer and Harper 2008).

Measurements of richness and diversity can be applied easily to palaeoecological data to examine the diversity recorded in death assemblages, providing insight into the relationship between a fossil assemblage and the contemporary living community. The technique encompasses two measures. The first, Richness, assesses how many species are represented in the assemblage and the second, Evenness, assesses the abundance of species relative to one another. For example, if one species constitutes 90% of an assemblage and nine other species constitute the remaining 10%, then this assemblage would be much less even than an assemblage where ten species each constitute 10% of the assemblage.

May (1975), Magurran (1988), Hammer and Harper (2008) and Lyman (2008) reviewed various methods of measuring ecological diversity and evenness within communities. The simplest measure of ecological diversity is the total number of species recorded, known as species richness. However, this metric usually underestimates the number of species that were actually present in the palaeo-community (Hammer and Harper 2008), and typically increases with sample size to a point of diminishing return. Several indices have been devised to compensate for these effects (see Magurran 1988; Hammer and Harper 2008; Lyman 2008). Other indices have been devised that attempt to describe the relationship between species richness and species abundance (diversity and evenness). Such measurements have proven useful in characterising, describing and comparing communities (Begon *et al.* 1986). However, because the nature of increasing biodiversity is dependent on the relative abundance of species, no one index can be considered universally ‘correct’ (Hammer and Harper 2008).

Quaternary sea-level change

Sea-level change during the Quaternary was primarily a consequence of the cyclic growth and decay of ice sheets in response to Milankovitch forcing insolation changes (Murray-Wallace 2007a, b). Observations of this variability provide constraints on the timing, rates, and magnitudes of the changes in ice mass during a glacial cycle (Short 1988; Fleming *et al.* 1998; Lambeck and Nakada 1990; Baker *et al.* 2001; Lambeck and Chappell 2001; Yokoyama *et al.* 2001; Barrows *et al.* 2002; Lambeck *et al.* 2002; Murray-Wallace 2007a, b; Reeves *et al.* 2008). Belperio *et al.* (2002) summarised Holocene sea-level studies conducted in Australia and reported rapid sea-level rise in the early Holocene, at about 16 mm/year, reaching present levels about 6.4 kyr ago. This was followed by regionally variable regression and emergence of the land of 1–3 m, a process that continues to the present (Belperio *et al.* 2002).

Several independent studies of sedimentary successions on continental shelves and shallow marine platforms such as Southern Australia (Ferland *et al.* 1995; Belperio *et al.* 2002), Bonaparte Gulf, northwestern Australia (Yokoyama *et al.* 2001), the Huon Peninsula, Papua New Guniea (Chappell 1974; Chappell *et al.* 1996; Chappell 2002) and Barbados (Steinen *et al.* 1973; Bard *et al.* 1990) have indicated a maximum sea-level lowering of between <130 and 121m during the Last Glacial Maximum (LGM) 22–17 kyr ago. These findings are consistent with other independent observations such as modelling global ice volumes and oxygen isotope evidence that place ice-equivalent sea-level between 135 and 120 m below present sea-level during the LGM (Clark and Mix 2002). The Barbados and Huon Peninsula relative sea-level records are particularly significant because they correlate so well, demonstrating that sea-level change occurred on a global level.

Limestone deposition and cave formation

On KI, Quaternary high stands were accompanied by the deposition of large coastal sand dunes, some of which migrated well inland to cover much of western and southern KI. Raised beaches and fossiliferous marine sediments at 3–5 m and 6–8 m above present sea-level indicate that at least two relatively higher sea-levels occurred during the Quaternary (Lampert 1981; Belperio and Flint 1999; Murray-Wallace 2002; Shand *et al*. 2006). During lower sea-levels, broken up shell and calcareous sands from the exposed sea floor were transported by onshore winds to form large fields of beach and backshore dunes. Many of these cemented into calcarenite to form parts of the Bridgewater group (Hill 1984; Twidale and Bourne, 2002; Shand *et al*. 2006).

Limestone caves and Rockshelters play an important role in the preservation of fossils. They provide shelter for mammalian and avian predators that concentrate the remains of prey and an alkaline environment that is conducive to bone preservation and fossilisation (Munoz-Duran and van Valkenburgh 2006). Limestone cave development is typically controlled by joints and fissures in hard rocks through which meteoric water can infiltrate to reach and react with ground water at the phreatic zone of (palaeo) water tables, resulting in limestone dissolution. Cave entrances can form by roof collapse or by dissolution along joints to form solution pipe or sinkhole entrances (Sprigg 1952; Jennings 1985). However, this is not how caves on KI have formed (Mooney 1983; Hill 1984; White 1994).

Prior to the deposition of Plio-Pleistocene dunes systems on KI, the lateritic plateau was drained by creeks and rivers on its northern and southern flanks (Twidale and Bourne, 2002; Shand *et al*. 2006). The genesis of calcarenite dunes impeded the plateaux existing drainage and led to the development of shallow lakes or swamps that held water above the Late Pliocene and Pleistocene dunes (e. g., at Kelly Hill). Overflow from these swamps drained into the calcaranite at influx points along the ridge, eroding cavities that eventually formed the caves (Mooney 1983; Hill 1984; Twidale and Bourne 2002). Water has never been observed draining out of these points and it presumably flows right through the base of the hill and discharges at the coast (Mooney 1983; Hill 1984).

Due to the porous nature of the calcarenite, lateral movement of groundwater into and under the hill has resulted in the solution of large lateral cavities approximately 25 metres beneath the top of the hill and deeper (Mooney 1983; Hill 1984). Immature caves found below this level tend to have flat to slightly domed roofs with an abundance of in-washed mud and few calcite decorations (Mooney 1983; Hill 1984). The mature domed-shaped caves that occur closer to the surface have developed by roof collapse as solution areas became too wide to support their own weight. Roof collapses continued until the roofs of caves assume a structurally stable arch, some of which open to the surface (Mooney 1983; Hill 1984). The unusual process of cave development is controlled by the soft, porous nature of the limestone and its lack of jointing, and the subterranean flow of swamp water into the base of the hill. The age of the cave system has not yet been determined, but probably dates back tens of thousands of years (Mooney 1983; Hill 1984).

Palaeontology on Kangaroo Island

Little literature is published regarding the palaeontology of KI. With the exception of Finlayson's (1938; 1963) work on Holocene fossils, palaeontological investigations are essentially restricted to Cambrian-aged invertebrates (e. g., Nedin 1995) and Pleistocene-aged megafauna from Black Creek Swamp, Flinders Chase National Park (Tindale *et al*. 1935; Hope *et al*. 1977; Wells *et al*. 2006; Grun *et al.* 2006; Forbes *et al.* 2009). Pledge (2002) reported cave surface collections made by members of the Cave Exploration Group of South Australia from Kelly Hill Caves, Emu Caves and Mount Taylor Cave as well as a sinkhole located on an Islet in Pelican Lagoon (Eastern KI) from which he reported *Rattus rattus* and *Oryctolagus cuniculus* (known to be a pet that was released in the islet) as well as native small mammals.

Archaeology on Kangaroo Island

The history of archaeology on KI was described by Cooper (1960), Lampert (1979; 1981), and Draper (1991; 1999). When the explorers Matthew Flinders and Nicolas Baudin first viewed KI, both independently remarked upon the lack of smoke that would indicate human presence (Lampert 1981). Radiocarbon dates from archaeological sites indicate that Aboriginals inhabited the island from at least 16 kyr ago until as recently as perhaps 0.4 kyr ago (Draper 1999). However, the majority of archaeological sites on KI are older than approximately 3 kyr (Draper 1999). The only mention of Indigenous vertebrate food remains on the island was recorded by Cooper and Condon (1947), who discovered a skull of *Potorous platyops* and emu egg shell in a midden at Pennington Bay. Other midden sites were recorded at West Bay, Little West Bay and Cape du Couedic, but at that time none were reported to contain vertebrate remains (Draper 1999). Tindale *et al*. (1935) recorded an association of stone tools with megafaunal remains from Rocky River, but did not suggest that as evidence of interaction. The only excavated evidence for the Aboriginal exploitation of vertebrate fauna on KI comes from two sources, Cape du Couedic and Seton Rockshelters (Hope *et al*. 1977; Lampert 1981; Draper 1999; Langeluddecke 2001).

Seton Rockshelter

Seton Rockshelter, located near the south coast toward the western end of the island on the shore of a freshwater lagoon (137° 03′ E, 35° 59′ S), was excavated in the early 1970’s by Ron Lampert. That assemblage represents the longest existing continuous temporal record of KI’s fauna as well as the earliest date of occupation by Aboriginals (Hope *et al.* 1977; Lampert 1981; Draper 1999). Aboriginals appear to have used the site periodically between approximately 16 and 10 kyr ago (Hope *et al.*

1977; Lampert 1981). Hope *et al.* (1977) concluded that when not occupied by humans, the shelter was used as a den by *Sarcophilus harrisii*. The fauna represented in the assemblage is quite different to that of modern KI. Several species represented in the Seton assemblage are locally extinct, but other species, now common on KI, were absent from the fossil record (Hope *et al.* 1977; Lampert 1981).

Hope *et al*. (1977) stated that the fauna of KI changed during the accumulation of the Seton assemblage, noting that the number of vertebrate species appeared to decline during the last 10 kyr. The number of marsupial species fell "from twenty or so to ten, and of those ten, three are known only from historical records" (Hope *et al*. 1977). Seven species of native rodents were recorded from the Seton site, but only three species can be found on KI today (Robinson *et al*. 2000).

Based on the known ecology of mammals, birds and reptiles excavated from Seton Rockshelter, Hope *et al*. (1977) interpreted that the Late Pleistocene environment of KI was cooler and drier than present and suggested that it supported areas of woodland, shrubland and heath, but must have also included "more extensive open vegetation, probably grassland, than today occurs naturally on KI" (Hope *et al*. 1977). In addition, Hope *et al*. (1977) ascribed the reduction in diversity to increased vegetation density at the expense of open grassland. However, they also reported a concurrent change of accumulation agent from *S. harrisii* to human. Therefore, the cause of the reduction in species diversity remains unclear, and might be due to a change in taphonomic bias associated with different accumulation agents.

Walshe (1996) was strongly critical of three features of Hope *et al.*'s (1977) interpretation. 1. the meaning of burnt bone, 2. bone fragmentation pattern and 3. the causes of change in species diversity in the assemblage. Walshe (1996) observed that the vast majority of burnt bone occurred in unit I where bones had been calcined, the result of being burnt at high temperature, probably in a hearth. In contrast, unit III contained almost no burnt bone. Walshe (1996) pointed out that in fact subunit m (situated directly below unit III) contained more burnt bone than unit III. In both cases bone had been blackened rather than calcined, indicating that it was burnt at a much lower temperature (Gilchrist and Mytum 1986; Spennemann and Colley 1989; Stine *et al*. 1995). Hope *et al*. (1977) interpreted that this was caused by the construction of fire pits or hearths on top of the bone, but Walshe (1996) posited that the bones could have been blackened by bushfire.

Hope *et al*. (1977) concluded that on the evidence of calcination and bone fragment size analysis, bone fragmentation in units II – IV was caused by *S. harrisii*, whereas bone fragmentation in unit I was caused by humans. However, bone fragmentation caused by *S. harrisii* and humans are challenging to differentiate and that measuring the percentage of fragment size categories by weight would not give an accurate result (Walshe 1996). In addition, size analysis was carried out on unidentified bone fragments only, potentially skewing the results (Walshe 1996).

Hope *et al*. (1977) determined that the lower units of the Seton assemblage were accumulated by *S. harrisii* rather than humans based on high species diversity, a high proportion of smaller bone fragments, a lack of burnt bone and the presence of *S. harrisii* remains in the deposit. Walshe (1996) agreed with the criteria used by Hope *et al*. (1977), but was not satisfied that other potential agents of accumulation were not ruled out. Hope *et al*. (1977) did not investigate the characteristics of bone accumulations made by *D. maculatus* nor *D. viverrinus* and stated that owls often contribute to accumulations made by *S. harrisii* but made no effort to determine whether owls contributed to the Seton assemblage, nor to what extent.

Cape du Couedic Rockshelter

Draper (1991) studied the Aboriginal archaeology of Cape du Couedic Rockshelter, but focused primarily on stone tool industries on KI. However, he did examine the bones of large mammals (primarily *Macropus fuliginosus*, *M. eugenii* and *Neophoca cinerea*) excavated from Cape du Couedic Rockshelter for cut marks that he attributed to butchering and hunting patterns. He found that 8% of the bones examined showed signs of burning, and 29% exhibited distinctive cut marks (Draper 1991). No attempt was made to study small vertebrates beyond the establishment of a species list (Draper 1991).

Draper (1991) observed that the bones of most of the smaller fauna were broken. He attributed this to rough handling by the original inhabitants of the site during butchering, cooking, chewing and disposal. However, only one bone was identified as having been gnawed by a human (Draper 1991). Tasmanian devils and quolls were ruled out as collection agents, but no other accumulating agents were examined.

Langeluddecke (2001) studied the small fauna excavated from Cape du Couedic Rockshelter. He reported that *Isoodon obesulus* and *Potorous platyops* was the most commonly occurring species but the fauna also included an unidentified wombat, three marsupial carnivores (*Sarcophilus harrisii*, *Dasyurus maculatus* and *Sminthopsis aitkeni*) and *Dromaius baudinianus* (represented by eggshell). Langeluddecke (2001) also reported that rodents, including *Pseudomys occidentalis*, *P. shortridgei*, *P. auritus* and *Rattus fuscipes*, were “By far the largest group represented in the assemblage…..” Langeluddecke (2001) concluded that Barn Owls were primarily responsible for part of the accumulation (trench two, level four) and may have been responsible for other parts of the assemblage. Langeluddecke (2001) could not detect any taphonomic pattern in the assemblage to indicate direct human interaction with, or exploitation of the small fauna. He hypothesised that the large amount of breakage throughout the assemblage and distortion of the owl assemblage was caused by human bioturbation. He summarised that the Cape du Couedic site experienced both cultural and non-cultural deposition of bone, but that both accumulations have been mixed by cultural practices including the digging and pit preparation of cooking hearth and site clean-up.

Summary

This literature review demonstrates the importance of studying Quaternary fossil deposits on islands. Isolation due to sea level rise can accentuate palaeoenvironmental changes on islands, potentially making them easier to detect. In addition, land-bridge islands can act as analogues for mainland vegetation fragmentation and may provide insight into the long-term effects of anthropic landscape modification. Predictions of global warming suggest that the preferred habitat of many animals will shift with changing climate or simply disappear, forcing many species to adapt or be extirpated. Therefore, in order to predict how animals will respond to future climate change it is vital that we understand how island-bound animals responded to it in the past.

Islands are important for conservation and natural resource management, frequently providing refugia for taxa that have been extirpated form their mainland range. These remnant populations may act as a source of individuals to be used in translocation programs, but fossil assemblages can provide much information regarding the richness, diversity and evenness of a community that a given (natural) environment can be expected to support. Knowledge of both the history and modern conditions under which taxonomic groups occur is essential to determine the conservation status of a given species and to make informed predictions regarding its future persistence. Furthermore, temporal changes of flora and fauna may provide information that can be used to predict the fate of mainland taxa in the event of future sea-level rise.

Coupled with other climate proxies (see Appendix 3) such as stable isotope analysis, pollen analysis, charcoal analysis and investigation of the chemical and physical characteristics of sediments and stratigraphy, the study of fossil fauna on KI will provide an enormous amount of information about its past, and potentially its future, biodiversity.

The timing and duration of KI's isolation from mainland Australia is well understood. However, in order to understand how climate change and island isolation has affected the fauna of KI, several questions must be addressed. These include the temporal pattern of late Pleistocene extinctions, the temporal pattern of extirpation of extant mammals, the temporal pattern of the arrival and departure of humans, the potential effects that the use of fire by humans may have had on flora and fauna. In addition, the taxonomy of genera that are difficult to differentiate using cranial anatomy alone (such as *Bettongia*) must be well understood. The study of previous and new fossil assemblages collected from KI will have critical implications for the understanding of the effects of climate change and insularity on one of southern Australia's most important nature conservation area.

CHAPTER 2

Re-evaluating the Late Quaternary mammal fossil assemblage of Seton Rockshelter, Kangaroo Island, South Australia, including the evidence for late-surviving megafauna

Context

This chapter documents the mammal fossil assemblage from Seton Rockshelter, the only reported Late Pleistocene–Holocene fossil mammal assemblage from Kangaroo Island.

Statement of Authorship

I confirmed and in some cases re-identified mammalian fossils from the Seton Rock Shelter assemblage (with support from those noted in the Acknowledgements). In addition, I reinterpreted the fossil assemblage and prepared the original and final manuscript for publication.

Gavin J. Prideaux commented on the manuscript and contributed to the discussion.

Keryn E. Walshe provided AMS radiocarbon ages commented on the manuscript and contributed to the discussion.

Re-evaluating the Late Quaternary mammal fossil assemblage of Seton Rockshelter, Kangaroo Island, South Australia, including the evidence for late-surviving megafauna

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Abstract

In light of the widespread view that most larger Australian vertebrates were extinct by 40 kyr ago, the recovery of sthenurine (short-faced) kangaroo remains from a layer yielding charcoal dated to 17 kyr ago in Seton Rock Shelter, Kangaroo Island, has proven contentious. Some researchers hold that the fossils are *in situ*, while others argue that they are reworked from older layers, necessitating further study of the site including direct dating of bone. Here we show that a series of radiocarbon ages on bone are consistent with the charcoal dates and in perfect depth order, which provides strong evidence for the stratigraphic integrity of the site. Taphonomic and palaeoecological analysis indicates that the 21–17 kyr units were primarily accumulated by Tasmanian devils and owls, before a switch to humans as collection agesnts after 17 kyr ago. Our analyses show that this taphonomic shift better explains faunal compositional changes than any ecological shifts prompted by climatic changes from the Late Pleistocene to Holocene. We argue that the remains of two sthenurine species in layers dated to 20–17 kyr are *in situ* based on the tight chronology, fossil preservation, faunal trends and a lack of older layers from which specimens could have been reworked. If corroborated by investigations of chronologically overlapping nearby sites, this would greatly extend the duration of the Pleistocene extinction event in Australia, and demands detailed re-evaluation of other sites for which post-40 kyr survival has been asserted.

Keywords: megafauna, extinction, radiocarbon dating, palaeo-environments

Introduction

Kangaroo Island (KI) is the third largest of Australia's land-bridge islands (Robinson 1999). It lies off the coast of South Australia on a broad expanse of the continental-shelf that extends about 100 km south of Eyre, Yorke and Fleurieu Peninsulas. Today it is isolated from Yorke and Fleurieu Peninsulas by Investigator Strait and Backstairs Passage, which reach depths of up to 40 m (Robinson and Armstrong 1999). KI retains the largest proportion (47%) of uncleared natural vegetation in any of the agricultural districts of southern Australia and has been spared the introduction of rabbits and foxes (Robinson 1999), making it one of Australia's most important nature conservation areas. KI was also the largest part of Australia not inhabited by Aborigines at the time of European colonisation, further reducing the degree of landscape modification (Lampert 1981; Walshe and Loy 2004). Consequently, KI may retain the best-preserved natural ecology in southern Australia. However, for all of its importance, little is known about the palaeofauna of KI, or how and when the modern composition of the fauna was established.

The Quaternary has been characterised by a generally increasing aridity coupled with global sea-level oscillations that have intermittently isolated KI from the mainland (Belperio and Flint 1999). During the late Pleistocene, KI was an elevated region on an exposed continental plain north of the continental-shelf (Belperio and Flint 1999; Draper 1999). During the Holocene, 125 m of rapid global sea-level rise occurred, isolating KI about 8.9 kyr ago and reaching present sea level about 7.5 kyr ago (Belperio and Flint 1999; Belperio *et al.* 2002). These events are expected to have had considerable impact on the vertebrate fauna of KI, which can only be observed by studying the fossil record.

Pleistocene mammal fossils have been reported from the Emu Caves (Pledge 2002) and Black Creek Swamp, Flinders Chase National Park (Tindale *et al.* 1935; Hope *et al.* 1977; Wells *et al.* 1999; Wells *et al.* 2006). However, Seton Rock Shelter, an archaeological assemblage excavated in the early 1970's by Dr R. Lampert is the only fossil assemblage on KI that bridges the Late Pleistocene and Holocene (Hope *et al.* 1977; Lampert 1981). Here we reinvestigate the continuity of the Seton Rock Shelter stratigraphy by radiocarbon dating bone from several stratigraphic layers. This is followed by a re-evaluation of the depositional taphonomy of the locality, context and interpretation of megafaunal remains, and veracity of the current palaeoenvironmental interpretation.

Seton Rock Shelter is located in the southwestern quadrant of KI near the shore of a freshwater lagoon (Fig. 1). This locality provides the longest continuous record of KI's fauna, as well as the earliest date for Aboriginal occupation (Hope *et al.* 1977;

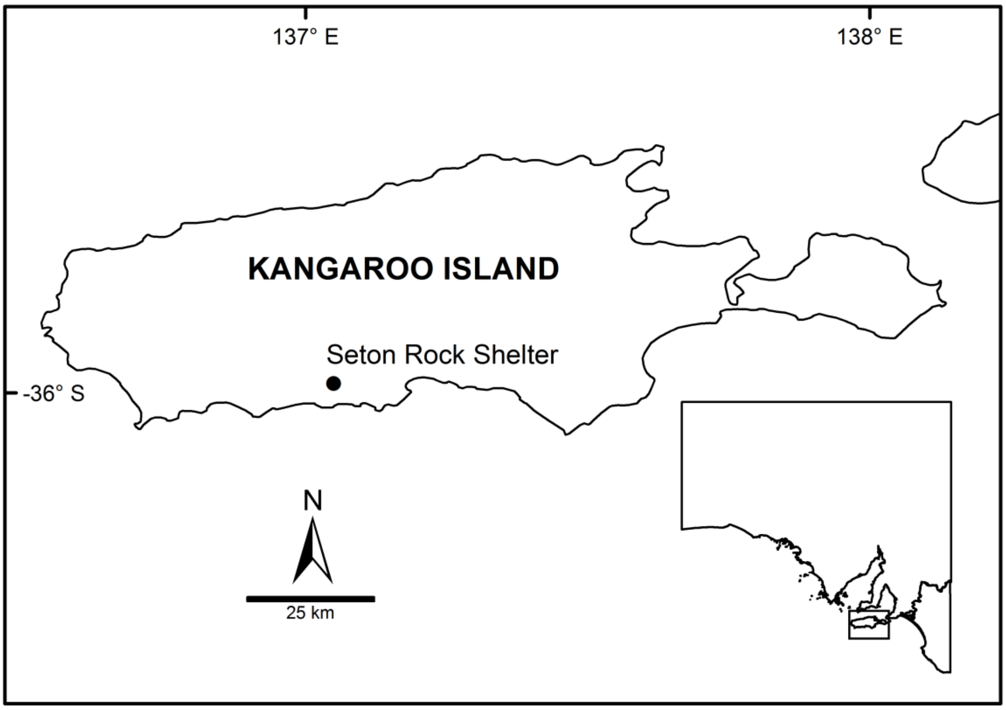

Fig. 1: Location of Seton Rock Shelter, Kangaroo Island.

Lampert 1981; Draper 1999). The presence of stone tools and radiocarbon dates on charcoal suggest that Aborigines may have used the site sporadically between 20 and 11 kyr ago (Hope *et al.* 1977; Lampert 1981), and used the site more intensively from 11 to 9.5 kyr ago. Hope *et al*. (1977) concluded that when unoccupied by humans, the shelter was used as a den by Tasmanian devils (*Sarcophilus harrisii*). They argued that differences in bone fragmentation suggested that *S. harrisii* accumulated units II–IV (subunits *o*–*g*), while humans accumulated unit I (subunits *f*–*a*). Subsequent researchers (Baynes *et al.* 1976; Baird 1991; Walshe 1994, 1996) showed that bone fragmentation caused by *S. harrisii* and humans is challenging to differentiate. Hope *et al*. (1977) also argued that differences in species diversity of the lower units of the Seton assemblage indicated accumulation by *S. harrisii* and that lower species diversity in the upper unit indicated accumulation by humans. At the same time, however, they also ascribed the change in species richness to the transition from the cooler, drier Late Pleistocene to the warmer, wetter Holocene.

In addition, Hope *et al*. (1977) did not investigate the possible contribution from owls and other carnivores as noted by Walshe (1996).

Fragments of sthenurine kangaroo teeth reported from Seton Rock Shelter by Hope *et al.* (1977), and dated to ca 20 kyr ago, have proven controversial in light of the wide acceptance of a pre-40 kyr date for the Australian Late Pleistocene extinctions. Some researchers argue that the teeth are poorly associated with the dated charcoal and likely reworked from older layers (Baynes 1999, Kershaw *et al.* 2000; Roberts *et al.*2001a; Roberts *et al.*2001b; Gillespie *et al.* 2006, 2012; Brook *et al.* 2007), while others believe that they represent an example of the late survival of some species (Trueman *et al*. 2005; Field 2006; Wroe and Field 2006, 2007; Flood 2007; Field *et al.* 2008). Johnson (2005) called for a re-evaluation of the Seton Rock Shelter assemblage to assess evidence for reworking and to validate its age using direct dating of bone. Questions raised by Walshe (1996), uncertainty surrounding the provenance of megafaunal remains, improvements in our knowledge of fossil identification and the advent of Accelerator Mass Spectrometer (AMS) radiocarbon dating of bone highlight the need for a reassessment of the Seton Rock Shelter assemblage.

Materials and Methods

Excavation

The current political climate precluded any new excavation of the Seton Rock Shelter site. Therefore, this investigation is based on existing material held in the Palaeontology collection of the South Australian Museum (SAM). Hope *et al.* (1977) reported that in 1971 an initial l m x 1.5 m test pit was dug inside the drip-line of the shelter. Later a one-metre square (designated K7), was excavated to bedrock and a second one-metre square (K6) was dug adjacent to the first and towards the back of the shelter.

Radiocarbon Dating

The validity of the stratigraphy was tested using AMS radiocarbon dating after permission for destructive analysis was granted by the SAM. Six postcranial bone samples were submitted to Rafter Radiocarbon Laboratory for AMS radiocarbon dating using a modified Longin method with filtration. Physical and chemical preparation processes followed those described by Beavan-Athfield and Sparks (2001). Age determinations, including those reported by Hope *et al.* (1977) were calibrated using OxCal 4.1.7 (Bronk-Ramsey 2009). Radiocarbon ages <11.0 cal. kyr BP were calibrated using the SHCal04 calibration curve (McCormac *et al.* 2004). Radiocarbon ages >11.0 cal. kyr BP were calibrated using the IntCal09 calibration curve (Reimer *et al.* 2009).

Species determinations

Diagnostic bones were re-identified using published descriptions and comparative material from the South Australian Museum Mammal and Palaeontology collections. Whole and partial crania, dentaries and teeth were used to identify specimens to the lowest taxonomic level possible (usually species). The minimum number of individuals (MNI) was determined by counting the number of the most common diagnostic element of each species in each spit across the entire excavation. This method is thought to minimise estimation biases caused by aggregation (Lyman *et al.* 2003). Nomenclature for extant and historically extinct mammals follows van Dyck and Strahan (2008) and nomenclature for sthenurine kangaroos follows Prideaux (2004).

Data analyses

To facilitate comparisons between subunits, MNI data were converted to relative abundances (Ri% = $MNI_{species}/MNI_{total}$ x 100), which were then plotted to detect trends in species abundance through time. To improve sample size, some stratigraphic subunits of similar age were pooled (*o–l*, *i–h*, *g–f*, *e–b*). These groupings largely conform to Lampert's (1981) stratigraphic units. Postcranial specimens from subunits g–f and subunits n–m were combined sometime in the past. As this was the only source of datable bone, those subunits were also grouped even though subunits g and f arise from different units. Subunit *a* is unfossiliferous. Species were also aggregated into ecological groups (after van Dyck and Strahan 2008) and plotted against time to explore ecological change. Stone tools hearths and calcined bone (which is present in unit I only) provide evidence of minimal human occupation of Seton Rockshelter. However, abundance of stone-tools (after Lampert 1981 p. 112, excluding waste flakes) provide an analogue for the intensity of human activity. Therefore, stone-tool frequency was plotted on a secondary axis to compare with ecological variance.

The raw data of grouped subunits and species (excluding indeterminate identifications) were analysed by correspondence analysis, which transforms both stratigraphic subunits and species to the same scale (Greenacre 2007; Dortch and Wright 2010), allowing the assessment of subunit-species relationships. Correspondence analysis scores for both subunits and species were then displayed using Ward's Method cluster analysis to determine which species characterise each stratigraphic subunit group. All statistics were carried out using PAST (Hammer *et al.* 2001).

Results

Dating

Five radiocarbon ages were obtained from postcranial bones submitted to Rafter Radiocarbon. All dates, including charcoal ages reported by Hope *et al.* (1977), have small errors and are entirely consistent with the stratigraphic sequence (Table 1). The sequence spans 20–9.5 kyr ago and strata appear to have accumulated at a relatively constant rate. An attempt to directly date a '*Procoptodon' gilli* (= *Sthenurus gilli*) tooth fragment was unsuccessful.

Table 1: Radiocarbon results and age estimates of bone and charcoal dated from Seton Rock Shelter, Kangaroo Island.

Lab Code	Material	Spit	Unit	Subunit	Conventional	Calibrated Age
NZA25830	Bone	K6/3a	I	c	9653±40	9.5–9.8
NZA25831	Bone	K6/3b	I	d	10430±40	10.3–10.6
ANU-925	Charcoal[2]	K6/4	I	e	10940±160	10.6–11.3
NZA25832	Bone	K6/6	I	f-g	13596±50	16.5–17.0
ANU-1221	Charcoal[2]	K6&7/14	III	l	16110±100	18.9–19.5
NZA25833	Bone	K6&7/14	III	l	17276±70	20.2–21.1
NZA25834	Bone	K6/15	IV	m-n	17450±75	20.4–21.3

Lab Codes: NZA = Rafter Radiocarbon, ANU = Australian National University
[1.] Calibrated age ranges and corresponding probability distribution function area percentages after projection of radiocarbon measurements onto calibration curves using the OxCal 4.1.7 programme (Bronk-Ramsey 2009). Radiocarbon ages <11.0 cal kyr BP were calibrated using the SHCal04 calibration curve (McCormac *et al.* 2004). Radiocarbon ages >11.0 cal kyr BP were calibrated using the IntCal09 calibration curve (Reimer *et al.* 2009). [2.] After Hope *et al.* (1977)

Table 2: MNI and Relative abundance of mammals recovered from Seton Rock Shelter, Kangaroo Island.

Aggregated subunits	l-o		k		j		h-i		f-g		b-e	
Species	MNI	Ri%	MNI	Ri%	MNI	Ri%	MNI	Ri%	MNI	Ri%	MNI	Ri%
Dasyurus maculatus	2	0.8	0	0.0	1	0.6	1	1.2	2	1.4	0	0.0
Dasyurus viverrinus	4	1.7	2	1.2	2	1.2	0	0.0	1	0.7	0	0.0
Dasyurus sp. indet.	6	2.5	4	2.4	1	0.6	0	0.0	1	0.7	0	0.0
Sarcophilus harrisii	2	0.8	1	0.6	1	0.6	2	2.4	2	1.4	1	1.9
Antechinus flavipes	0	0.0	1	0.6	0	0.0	0	0.0	0	0.0	0	0.0
Antechinus sp. indet.	1	0.4	1	0.6	0	0.0	0	0.0	0	0.0	0	0.0
Sminthopsis aitkeni	3	1.3	7	4.2	2	1.2	2	2.4	0	0.0	0	0.0
Sminthopsis crassicaudata	1	0.4	1	0.6	1	0.6	1	1.2	0	0.0	0	0.0
Sminthopsis sp. indet.	5	2.1	3	1.8	1	0.6	2	2.4	1	0.7	0	0.0
Isoodon obesulus	3	1.3	2	1.2	3	1.7	0	0.0	4	2.8	8	14.8
Perameles bougainville	5	2.1	3	1.8	2	1.2	0	0.0	1	0.7	0	0.0
Peramelidae sp. indet.	7	3.0	2	1.2	5	2.9	3	3.6	1	0.7	6	11.1
Phascolarctos cinereus	1	0.4	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
Lasiorhinus latifrons	2	0.8	2	1.2	1	0.6	1	1.2	1	0.7	0	0.0
Trichosurus vulpecula	0	0.0	0	0.0	0	0.0	0	0.0	1	0.7	2	3.7
Bettongia lesueur	2	0.8	1	0.6	1	0.6	1	1.2	1	0.7	1	1.9
Bettongia penicillata	13	5.5	13	7.8	10	5.8	2	2.4	7	5.0	2	3.7
Bettongia sp. indet.	4	1.7	4	2.4	0	0.0	1	1.2	2	1.4	3	5.6
Potorous platyops	11	4.7	6	3.6	11	6.4	4	4.8	6	4.3	2	3.7
Lagorchestes leporides	13	5.5	9	5.4	6	3.5	2	2.4	11	7.8	1	1.9
Macropus eugenii	1	0.4	1	0.6	0	0.0	0	0.0	0	0.0	0	0.0
Macropus greyi	2	0.8	1	0.6	2	1.2	1	1.2	2	1.4	2	3.7
Macropus rufogriseus	2	0.8	2	1.2	2	1.2	1	1.2	2	1.4	1	1.9
Macropus fuliginosus	1	0.4	0	0.0	2	1.2	2	2.4	0	0.0	6	11.1
Macropus (Osphranter) sp. indet.	0	0.0	1	0.6	1	0.6	0	0.0	1	0.7	0	0.0
MACROPODIDAE spp. indet.	5	2.1	0	0.0	0	0.0	0	0.0	1	0.7	3	5.6
Onychogalea fraenata	2	0.8	0	0.0	0	0.0	1	1.2	2	1.4	0	0.0
Lagostrophus fasciatus	1	0.4	0	0.0	1	0.6	0	0.0	0	0.0	0	0.0
"Procoptodon" gilli	3	1.3	0	0.0	0	0.0	0	0.0	0	0.0	0	0.0
"Procoptodon" browneorum	0	0.0	0	0.0	0	0.0	0	0.0	1	0.7	0	0.0
Cercartetus lepidus	1	0.4	0	0.0	1	0.6	0	0.0	0	0.0	0	0.0
Hydromys chrysogaster	0	0.0	0	0.0	1	0.6	0	0.0	0	0.0	0	0.0
Mastacomys fuscus	32	13.6	21	12.6	23	13.3	12	14.3	17	12.1	1	1.9
Pseudomys auritus	18	7.6	3	1.8	22	12.7	7	8.3	13	9.2	2	3.7
Pseudomys occidentalis	36	15.3	28	16.8	32	18.5	11	13.1	18	12.8	2	3.7
Pseudomys shortridgei	16	6.8	21	12.6	19	11.0	11	13.1	19	13.5	3	5.6
Pseudomys sp. indet.	5	2.1	6	3.6	7	4.0	4	4.8	8	5.7	0	0.0
Rattus fuscipes	6	2.5	10	6.0	2	1.2	10	11.9	10	7.1	4	7.4
Rattus lutreolus	15	6.4	11	6.6	7	4.0	2	2.4	4	2.8	4	7.4
Rattus sp. indet.	5	2.1	0	0.0	3	1.7	0	0.0	1	0.7	0	0.0
Totals	236	100	167	100	173	100	84	100	141	100	54	100

Species determinations

Most of the species identified by Hope *et al.* (1977) from Seton Rock Shelter were confirmed here, but we also recognised several species hitherto not recorded (*Sminthopsis aitkeni*, *S. crassicaudata*, *Macropus eugenii*, *Lagostrophus fasciatus*, *Onychogalea fraenata* and *'Procoptodon' browneorum*; Table 2). Hope *et al.* (1977) identified *Macropus rufus* (= *Megaleia rufa*) in the Seton assemblage, which would be consistent with the known extension of this species to the southern periphery of the mainland (Reed and Bourne 2009), presumably during the last glacial maximum. From our assessment of the Seton molar fragments, however, we were unable to identify any traits that allowed their distinction lower than the level of subgenus *Osphranter*. *Macropus eugenii* was represented by only two individuals, and other macropodids were also relatively rare.

Species Abundance and Ecology

Macropodids, bandicoots and possums have higher relative abundances in subunits *e–b*, which also contain the majority of stone tools (Fig.2a). In contrast, *Dasyurus* spp., *S. harrisii* and *Sminthopsis* spp. (Fig.2b) and *Mastacomys fuscus*, *Pseudomys australis*, *P. occidentalis* and *P. shortridgei* decrease in relative abundance in the upper subunits (Fig.2c). When aggregated into ecological guilds (Fig.2d) there appears to have been little faunal variation until humans began to use the site intensively (as indicated by stone tools).

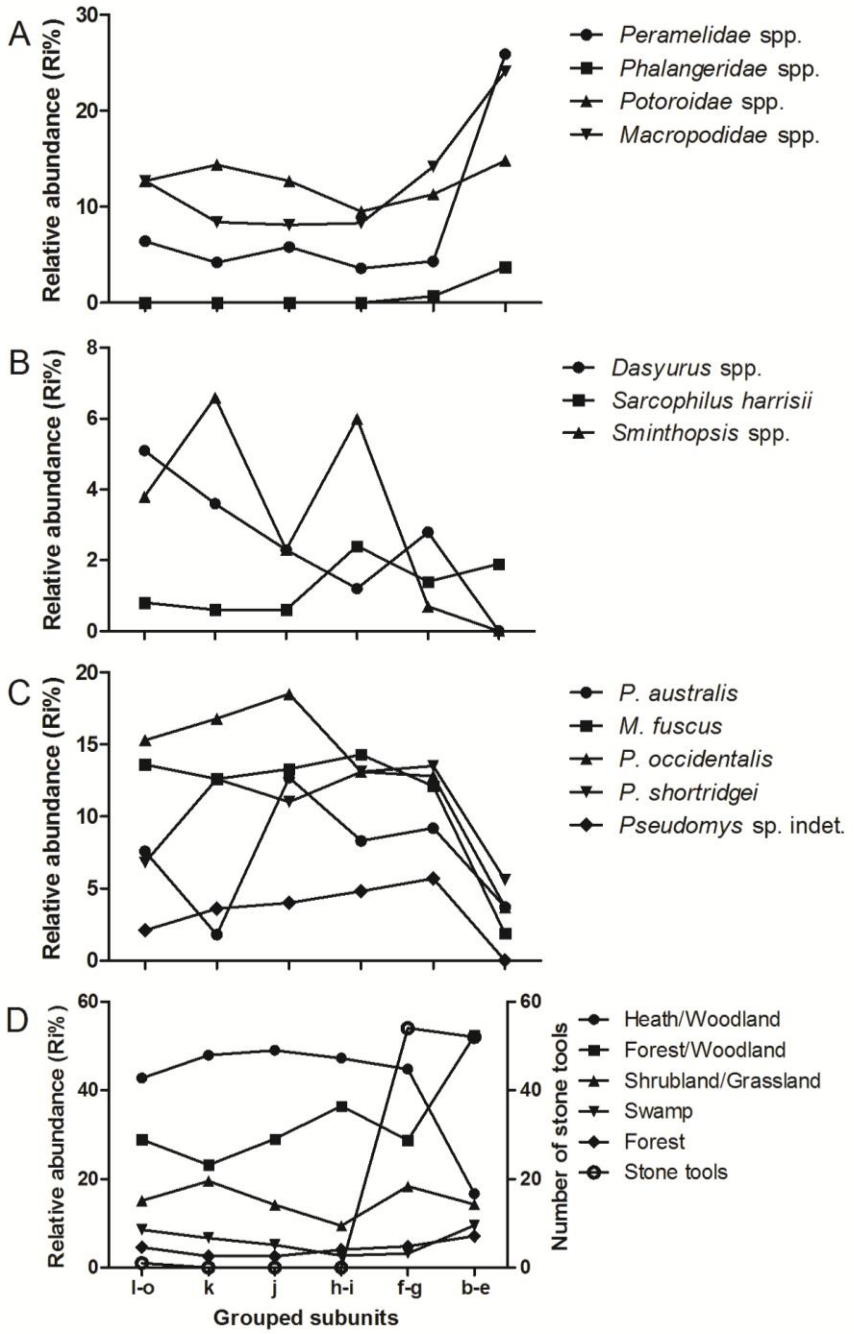

Fig.2a-d: Relative abundance graphs of selected species and aggregated ecological guilds

Table 3: Eigenvalue and variance accounted for by each axis of correspondence analysis

Axis	Eigenvalue	Variance (%)
1	0.258481	66.575
2	0.0431814	11.122
3	0.0343029	8.8352
4	0.0314308	8.0954
5	0.0208575	5.3721

Correspondence analysis

The first three axes of the correspondence analysis account for almost 85% of the variance in the original table (Table 3). However, the scree slope of eigenvalues for each correspondence axis (Fig. 3) indicates that axis 1 accounts for most of the variation in the original data. The slope of the line levels off at axis 2 indicating subsequent axes are of little importance. The correspondence analysis scatter plot (Fig. 4) shows that subunit group *b–e* has a high positive axis 1 value relative to other subunits and clusters loosely with *Isoodon obesulus*, *Macropus fuliginosus*, *T. vulpecula* and stone tools. All other subunits align along axis 2 and plot nearer the centroid, clustering with the majority of the remaining species. This indicates substantial differences in the faunal composition of subunits *e–b* and all deeper subunits.

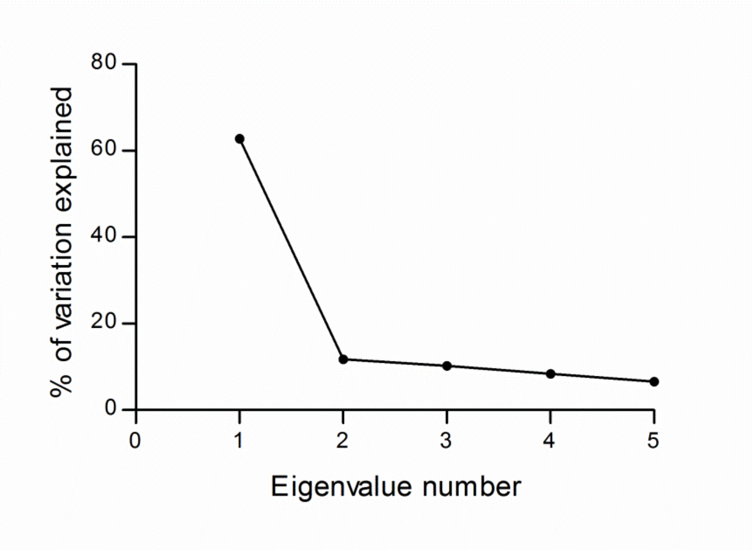

Fig. 3: Scree plots of eigenvalues for each correspondence axis, showing that the first vector accounts for most of the variation and that the line levels off at CA2 indicating subsequent vectors are of little substantive importance.

Megafauna

Reanalysis confirmed that the sthenurine tooth fragments recognised by Hope *et al.* (1977) were indeed '*P.*' *gilli*, but here we also recognise a second sthenurine species, '*Procoptodon*' *browneorum,* from subunit *f*. Bone from this subunit has been dated to 17.0–16.5 cal kyr BP. All sthenurine specimens originate from what Hope *et al*. (1977) refer to as 'black culturally rich soil horizons'. The largest specimen of '*P.*' *gilli* did not preserve enough collagen to radiocarbon date directly. However, bone from subunit *l* yielded an AMS radiocarbon age of 21.1–20.2 cal kyr BP which compares well with Hope *et al*.'s (1977) charcoal age of 19.5–18.9 cal kyr BP.

Discussion

Collection agents and species abundance

Palaeo-environmental interpretation of assemblages accumulated by both human and non-human collection agents normally requires a good understanding of their taphonomy. However, taphonomic histories of such assemblages are hard to interpret (Dortch and Wright 2010 and references therein). With the exception of sporadic tooth marks occasionally left by *S. harrisii*, it is difficult to differentiate between *S. harrisii* and human accumulations based on bone modification (Baynes *et al.* 1976; Walshe 1996; Dortch and Wright 2010). Therefore, faunal composition may be useful to distinguish between fossils accumulated by *S. harrisii* and humans. *S. harrisii* is a poor predator but an excellent scavenger that collects a wide range of the animals that die around bone accumulation sites. In addition, *S. harrisii* frequently use rock shelters and caves as latrines as a form of social communication (Walshe 1996). The traditional diet of Australian Aboriginals included a diverse range of plants and animals of all sizes (e. g. Meagher 1974; Hiatt 1978; Naughton *et al*. 1986; O'Dea *et al*. 1991; Miller *et al*. 1993). However, animal carcases may have been prepared and cooked in the open air rather than in rockshelters and large animals such as kangaroos may have been butchered at kill sites (Garvey 2010). Consequently, representation of animal prey in the assemblage may not represent the full breadth of species hunted.

High faunal diversity, occasional tooth marks and a lack of stone tools point to *S. harrisii* as the primary accumulating agent of subunits *o–f*, confirming the interpretation of Hope *et al*. (1977). However, the high abundance of rodents relative to larger mammals (Table 2) also suggests that owls also made a significant contribution. By comparison, subunits *e–b* contains a much narrower spectrum of species (Fig. 2a–d). The comparative paucity of rodents in subunits *e–b* suggests a reduction in owl accumulated prey in the assemblage and coincides with the increase of stone tool frequency that suggests an intensification of human occupation of the rockshelter. This interpretation is supported by correspondence analysis (Fig. 4), which shows a strong negative relationship between subunit groups and Axis 2 and an association between *M. fuliginosus*, *I. obesulus*, *T. vulpecula* and stone tools (Fig. 4). Cluster analysis (Fig. 5) offers further support that the dominant species in subunits *e–b* increase along with stone tools.

Palaeoenvironmental interpretation

The composition of the Seton Rock Shelter mammal assemblage differs from that of the modern KI fauna. *Macropus eugenii* (MNI = 2) is rare in the Seton assemblage (Table 2), but extremely common on KI today. If *M. eugenii* was a significant presence in the palaeocommunity it is likely that both *S. harrisii* and

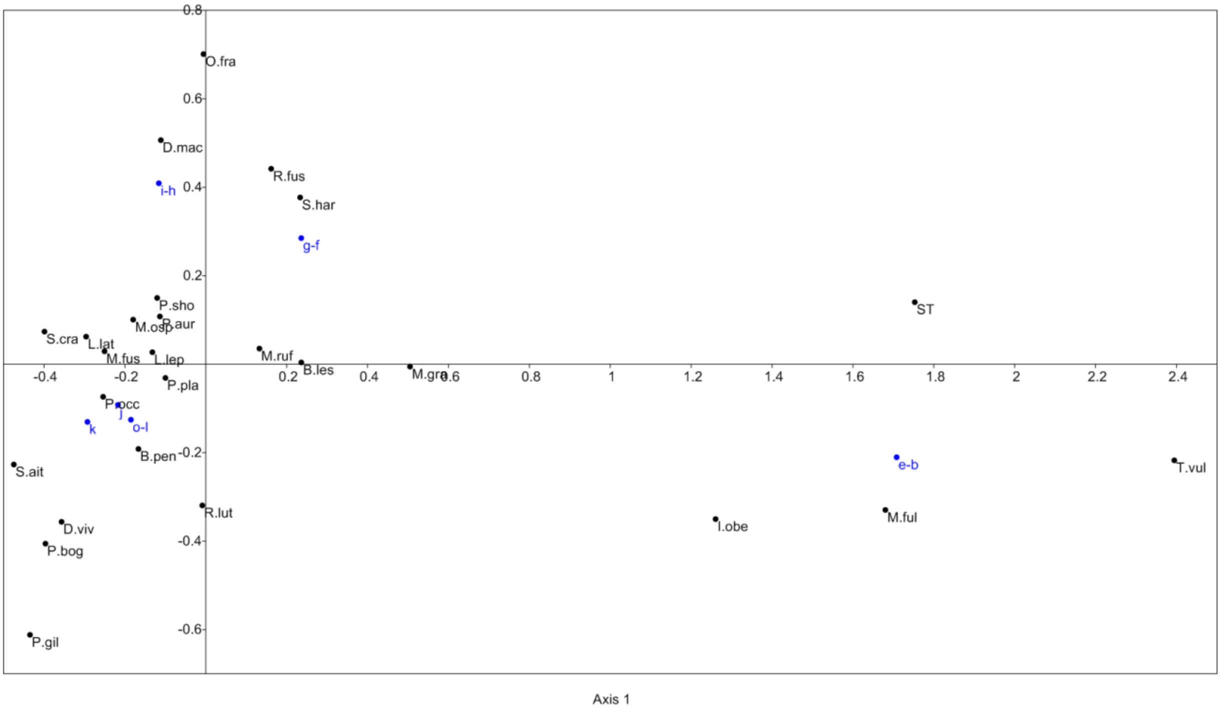

Fig. 4: Correspondence Analysis scater plot of Seton Rock Shelter MNI and stone tool data.

ST = stone tools, D.mac = *Dasyurus maculatus*, D.viv = *Dasyurus viverrinus*, S.har = *Sarcophilus harrisii*, A.fla = *Antechinus flavipes*, S.ait = *Sminthopsis aitkeni*, S.cra = *Sminthopsis crassicaudata*, I.obe = *Isoodon obesulus*, P.bog = *Perameles bougainville*, P.cin = *Phascolarctos cinereus*, L.lat = *Lasiorhinus latifrons*, T.vul = *Trichosurus vulpecula*, B.les = *Bettongia lesueur*, B.pen = *Bettongia penicillata*, P.pla = *Potorous platyops*, L.lep = *Lagorchestes leporides*, M.eug = *Macropus eugenii*, M.gra = *Macropus greyi*, M.ruf = *Macropus rufogriseus*, M.ful = *Macropus fuliginosus*, M.osp = *Macropus* (*Osphranter*) sp. indet., O.fra = *Onychogalea fraenata*, L.fas = *Lagostrophus fasciatus*, P.gil = *'Procoptodon' gilli*, P.bro = *'Procoptodon' browneorum*, C.lep = *Cercartetus lepidus*, H.chr = *Hydromys chrysogaster*, M.fus = *Mastacomys fuscus*, P.aus = *Pseudomys australis*, P.occ = *Pseudomys occidentalis*, P.sho = *Pseudomys shortridgei*, R.fus = *Rattus fuscipes* and R.lut = *Rattus lutreolus*.

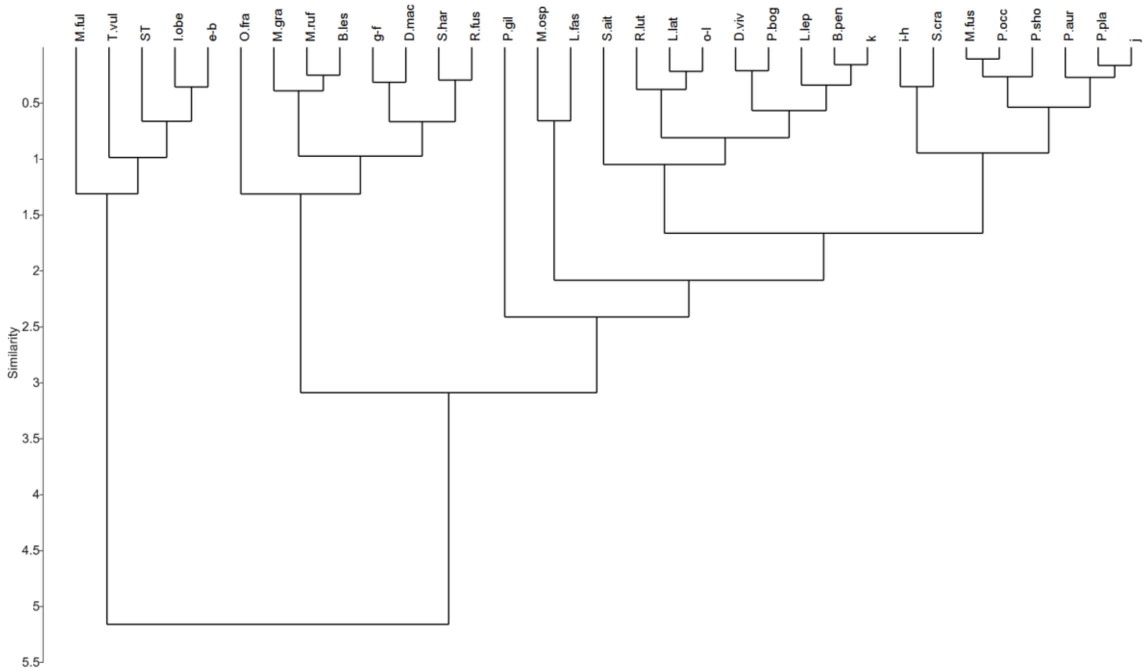

Fig. 5: Ward's Method Cluster analysis of correspondence analysis scores.

ST = stone tools, D.mac = *Dasyurus maculatus*, D.viv = *Dasyurus viverrinus*, S.har = *Sarcophilus harrisii*, A.fla = *Antechinus flavipes*, S.ait = *Sminthopsis aitkeni*, S.cra = *Sminthopsis crassicaudata*, I.obe = *Isoodon obesulus*, P.bog = *Perameles bougainville*, P.cin = *Phascolarctos cinereus*, L.lat = *Lasiorhinus latifrons*, T.vul = *Trichosurus vulpecula*, B.les = *Bettongia lesueur*, B.pen = *Bettongia penicillata*, P.pla = *Potorous platyops*, L.lep = *Lagorchestes leporides*, M.eug = *Macropus eugenii*, M.gra = *Macropus greyi*, M.ruf = *Macropus rufogriseus*, M.ful = *Macropus fuliginosus*, M.osp = *Macropus* (*Osphranter*) sp. indet., O.fra = *Onychogalea fraenata*, L.fas = *Lagostrophus fasciatus*, P.gil = *'Procoptodon' gilli*, P.bro = *'Procoptodon' browneorum*, C.lep = *Cercartetus lepidus*, H.chr = *Hydromys chrysogaster*, M.fus = *Mastacomys fuscus*, P.aus = *Pseudomys australis*, P.occ = *Pseudomys occidentalis*, P.sho = *Pseudomys shortridgei*, R.fus = *Rattus fuscipes* and R.lut = *Rattus lutreolus*.

humans would have incorporated it into the Seton assemblage. Therefore the rarity of *M. eugenii* in the fossil record is probably an accurate reflection of its abundance in the palaeofauna. Based on the modern ecology of mammal species excavated from Seton, Hope *et al.* (1977) envisaged a Late Pleistocene environment that was cooler and drier than present. They suggested that it supported areas of woodland, shrubland and heath, in addition to more extensive open grassland vegetation than naturally occurs on KI today. Hope *et al.* (1977) also ascribed the reduction in species diversity to increased vegetation density at the expense of open grassland. Changes in the guild structure of the Seton fauna (Fig. 2d) coincide with the presence of stone tools in the stratigraphy, which indicates that the apparent changes in fauna and species richness (Table 2) is probably related to a change in collection agent rather than climate. This interpretation is supported by correspondence and cluster analyses (Figs. 4–5).

Radiocarbon dating and megafauna

The exact match between radiocarbon dates and the stratigraphic sequence strongly suggest that little reworking has occurred in the deposit. Even though the few megafauna specimens recovered from the site are highly fragmented, it is critical to note that fossils of all other taxa are also highly fragmented. Fossil fragmentation is related to the agents of accumulation; it does not, in and of itself, constitute evidence of reworking from older strata. There is no sound logical basis to assert *a priori* that fragments of extinct species should be deemed any more likely to have been reworked than those of equally fragmentary species that remain extant. Evidence for reworking must be established on other taphonomic as well as geochronological grounds.

Conclusion

Can we say, then, that the new evidence corroborates the view that sthenurine kangaroos survived on KI to well beyond 40 kyr ago? Indirect dating evidence supports the argument that the sthenurine fossils are *in situ*, suggesting that they may have survived well after Aboriginals colonised Australia. However, resolution of the problem is hampered by the inability to directly date the extinct species. The fragmentary nature of the megafauna remains is consistent with the remains of extant species from the site but makes it all but impossible to determine depositional contemporaneity. We therefore argue that because the question cannot be resolved based on evidence obtained from Seton alone, that the site should be disregarded in further discussion of Pleistocene extinctions. However, the suggestion of late surviving megafauna on KI remains tantalizing and demands further exploration and research of other fossil accumulations on KI.

Acknowledgements

Mary-Anne Binnie, Catherine Kemper and David Stemmer kindly provided access to the Palaeontology and Mammal Collections of the South Australian Museum. We thank Jeannette Hope, Rachel Correll, Grant Gully, Amy Macken and Graham Medlin for insightful discussions and Joe Dortch for advice on statistics.

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CHAPTER 3

The elevation of *Bettongia anhydra* (Marsupialia: Macropodidae) to specific status

Context

To ensure accurate identification of bettongs recovered from Kelly Hill Cave (5K1), craniodental characteristics of the genus were careful interrogated. Examination of modern and fossil specimens housed in the South Australian and Western Australian Museums lead to the realisation that *Bettongia anhydra* was morphologically distinct from other bettongs. This manuscript provides a morphological description of *Bettongia* that will be combined with ancient DNA data to produce a collaborative paper that explores the taxonomy of the genus.

Statement of Authorship

I examined modern and fossil bettong specimens, compared the morphology of extant and recently extinct bettongs and described the Holotype of *Bettongia anhydra*.

Gavin J. Prideaux provided guidance and advice, commented on the draft manuscript and contributed to the discussion.

Alexander Baynes helped locate and identify *Bettongia* specimens in the Western Australian Museum palaeontology collection, provided guidance and advice, commented on the draft manuscript and contributed to the discussion.

The elevation of *Bettongia anhydra* (Marsupialia: Macropodidae) to specific status

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Abstract

In 1933 Michael Terry collected the skull from a small macropodid captured near Lake Mackay in the western Northern Territory. First described as a new sub-species of the Brush-tailed Bettong, *Bettongia penicillata anhydra*, it was later synonymised with *Bettongia lesueur*. Newly examined material from Holocene aged Western Australian cave accumulations share markedly similar craniodental morphology to the Lake Mackay specimen, and confirm sufficient distinction from all other species of *Bettongia* to warrant separation at the specific level. *Bettongia anhydra* is most similar to *Bettongia lesueur* but differs in premolar shape, rostrum length, dentary proportions and molar size gradient. The elevation of this recently extinct bettong to full species suggests that Australia's biodiversity loss may be greater than currently believed. All *Bettongia* spp. have experienced extensive range contractions since European colonisation and some now persist on Islands only. Bettongs (along with Potoroos and Peramelids) perform valuable eco-services that improve soil structure and water infiltration and retention. They also play an important role in the dispersal of seeds and fungal spores, facilitating symbiotic relationships between fungi and numerous vascular plants species that are essential for plant recruitment and

vegetation succession. Therefore, the near total loss of these ground-foraging mammals from the Australian landscape is particularly devastating and has far reaching ecological implications.

Introduction

Bettongs, commonly known as rat-kangaroos, are small to medium nocturnal marsupials that occupy a basal branch within the Macropodidae (Prideaux and Warburton 2009). They retain plesiomorphic kangaroo characteristics such as a prehensile tail, less reduced forelimbs, well developed upper canines, large blade-like premolars and less specialised molars (Claridge *et al*. 2007). With the possible exception of *Bettongia lesusur* which mainly eats roots and tubers, bettongs primarily eat hypogeal fungi (Seebeck and Rose 1989; Claridge *et al*. 2007) and in doing so help to maintain soft, friable, well-structured topsoil (Martin 2003; Eldridge 2009; Eldridge *et al*. 2012). Bettongs were once broadly distributed across Australia, but since European colonisation almost all bettongs have contracted to a fraction of their former ranges. Morphological (Tate 1948; Flannery and Archer 1987; Flannery 1989; Prideaux 1999) and molecular (Westerman *et al.* 2002, 2004; Meredith *et al.* 2008) phylogenetic data indicate that within the extant Potoroinae, *Bettongia* is most closely related to *Aepyprymnus* to the exclusion of *Potorous*. *Bettongia* currently includes four extant and two (one Holocene and one Miocene aged) extinct species. Taxonomy of the genus was partially revised by Finlayson (1958) and more comprehensively by Wakefield (1967), who raised *B. tropica* from what had hitherto been considered a northern equivalent of *B. penicillata*. Most recently, two fossil species have been added: *Bettongia moyesi* from the Miocene Riversleigh deposit in northwestern Queensland (Flannery and Archer 1987) and *Bettongia pusilla* from Holocene cave deposits of the Nullarbor Plain (McNamara 1997).

Finlayson (1957) described two new subspecies of Brush-tailed Bettong; *Bettongia penicillata francisca*, the holotype reportedly from St Francis Island, Nuyts Archipelago, South Australia, and *B. p. anhydra*, the holotype and only known specimen of which was collected by explorer Michael Terry from McEwin Hills near Lake Mackay in the western Northern Territory. Aitken (1976) noted that the holotype of *B. p. francisca* lacked provenance data and questioned Finlayson's knowledge of the origin of the specimen. This subspecies is now considered a junior synonym of *B. p. penicillata* (Aitken 1976). Finlayson (1957, p. 553) described *B. p. anhydra* as "a remarkable blend of *penicillata* and *lesueuri* [sic] characters". Wakefield (1967) observed that several features of the specimen, including its short rostrum, very large bullae and proportionately long premolars indicated that *B. p. anhydra* should be reallocated to *B. lesueur*. During part of a larger study on bettong taxonomy and distribution, we recently observed Holocene fossil specimens in the Western Australian Museum that are more consistent in craniodental morphology with the Lake Mackay specimen than with either *B. penicillata* or *B. lesueur*. We concur with Finlayson (1957, p. 554), who stated that "if its dual character were confirmed in series, it [*B. p. anhydra*] would merit specific recognition", and herein raise *B. anhydra* to full specific status, and provide a new diagnosis and comparison. Phylogenetic implication of *B. anhydra* will be dealt with in a forthcoming study synthesising morphological and molecular data within the Potoroinae.

Methods

The holotype of *Bettongia anhydra* is registered in the Mammal Collection of the South Australian Museum. The following abbreviations are used in this paper: FUR = Flinders University of South Australia reference collection; SAM = South Australian Museum (M: Mammal Collection; P: Palaeontological Collection); WAM = Western Australian Museum Palaeontological Collection. Dental homology, nomenclature and family-group taxonomy follows Prideaux (2004) and Prideaux and Warburton (2010). Specimens used for comparison with *Bettongia anhydra* can be found in the Supplementary Information.

Systematics

Order Diprotodontia Owen 1866

Superfamily Macropodoidea Gray 1821

Family Macropodidae Gray 1821

Subfamily Potoroinae Gray 1821

Tribe Bettongini Flannery and Archer 1987

Genus *Bettongia* Gray 1837

Revised diagnosis of Bettongini

Tribe Bettongini includes species of *Bettongia*, *Caloprymnus*, *Aepyprymnus* and *Milliyowi*. Bettongins can be differentiated from members of the tribe Potoroini (containing *Potorous*) based on the following characters: cranium bears postglenoid process and discrete periotic ectotympanic process. I3 short crowned. P3 bears many fine vertical ridgelets. Buccal crests of upper molars better developed than lingual counterparts. Dentaries stout with convex ventral margin. I1 lacks a dorsal and ventral enamel flange. P3 bears many vertical ridgelets. Lingual crests of lower molars better developed than buccal counterparts.

Revised diagnosis of *Bettongia*

Species of *Bettongia* are united by only one synapomorphy: jugal extends dorsally to at least level of large lachrymal foramen. However, they can be further differentiated from species of *Caloprymnus* and *Aepyprymnus* by their combined possession of large posterior palatal vacuities, inflated auditory bullae and P3/p3 with six or more vertical ridgelets.

Bettongia anhydra Finlayson 1957

Synonyms: *Bettongia penicillata anhydra*

Holotype

Near-complete adult cranium (SAM M3582) with associated left and right dentaries collected from a fresh carcass by Michael Terry in 1933 from the McEwin Hills area, near Lake Mackay, Northern Territory. Cranium lacks occipitals, basioccipitals, paroccipital processes and part of the left squamosal; tympanic bullae are broken but enough is preserved to infer shape and degree of inflation. Left dentary complete, though m4 absent. Right dentary articular process not preserved.

Type locality

McEwin Hills, Lake MacKay area, Northern Territory, approximately 22° 2' S, 129° 47' E (Fig. 1).

Referred Specimens

Unnamed cave, Eucla Basin: WAM 67.10.530, adult left maxilla with P3 and M1-3.

Cocklebiddy Cave Eucla Basin: WAM 68.2.166, part adult right dentary with m1-3, horizontal & ascending rami damaged.

Unnamed rock shelter, Merkamoota (?Merkanooka) Station, Morawa: WAM 66.1.7a, adult left maxilla with P3 and M1-4; WAM 66.1.7b, adult right maxilla, with P3 and M1-2 (see Fig. 1).

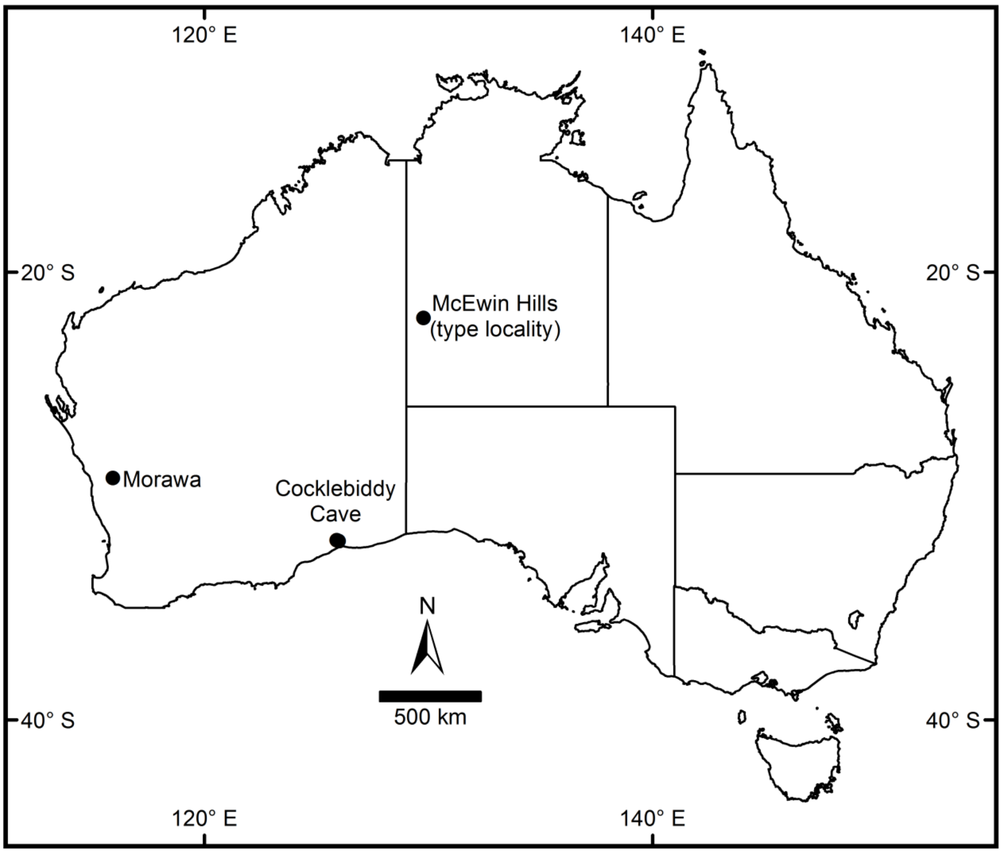

Fig. 1: Location of type and referred specimens (where coordinates could be determined) of *Bettongia anhydra*.

Diagnosis

Bettongia anhydra can be distinguished from all other bettongs by the following features; highly developed posterior molar gradient (M1 ≤ M2 > M3 >> M4) and highly reduced fourth molars; anteroposterior compression of rostrum, high degree of interorbital constriction; obscuration of m4, m3 hypolophid and part of m3 protolophid by ascending ramus in lateral view.

It can be further separated from *B. gaimardi*, *B. penicillata* and *B. tropica* by high inflation of auditory bullae (similar to *B. lesueur*); *B. pusilla* which has higher crowned, more lophodont, equal sized molars; *B. gaimardi*, *B. lesueur*, *B. moyesi*, *B. pusilla* and *B. tropica* by greater buccal flexation of anterior third of P3; *B. penicillata* by lesser flexation of anterior third of P3. Dentary differs from *B. gaimardi*, *B. lesueur*, *B. penicillata* and *B. pusilla* in robustness of horizontal ramus and anterior occurrence of digastric eminence; *B. gaimardi, B. moysei*, *B. penicillata*, *B. pusilla* and *B. tropica* in length and breadth of coronoid process and acute angle between ascending ramus and horizontal ramus.

Description

All features in referred specimens are as for holotype. No juvenile or postcranial specimens known.

Cranium—Holotype with short premaxilla; upright portion essentially vertical. Anterior edge of premaxilla slightly arcuate in lateral view (Fig. 2a, d). Diastema very short, straight and only slightly deflected anteroventrally relative to cheek tooth row; maxilla contributes to most of diastema length. I1 high crowned and peg shaped, I2 and I3 comparatively elongated anteroposteriorly. C1 well-developed. Anterior palatal foramina broad and short, posterior terminus occurs just past anterior edge of C1 alveolus (Fig. 2b). Rostrum very short and deep rapidly tapers anteriorly, with lateral edges enclosing an angle of 20° (Figs.2b, c). Premaxilla contributes approximately half of length of lateral surface of rostrum. Narial aperture deeper than broad (Fig. 2a, d). Buccinator fossa shallow, restricted to ventral half of lateral surface of rostrum and extending from anterior edge of P3 anterior root to posterior of C1 alveolus. Masseteric process short and composed entirely of maxilla, positioned adjacent to M1 protoloph (Fig. 2a, d). Infraorbital foramen opens anteriorly; positioned directly above posterior root of P3 at level of ventral border of orbit. Small posterior (dorsal) lacrimal foramen opens dorsally; separated from larger anterior (ventral) lacrimal foramen by large lacrimal tuberosity which marks anterodorsal extremity of orbital rim. Anterior nasals exceptionally narrow constricting at maxilla-pre-maxilla suture. Nasal-frontal sutures arcuate extending posterior of the anterior edge of the orbit. Palatine bones well developed, large posterior palatal foramina originate adjacent to metaloph of M1 and extend posteriorly remaining length of palate (Fig. 2b). Temporal (parietal) crests weakly developed, confluent anteriorly with supraorbital crests, and terminating posteriorly at triangular interparietal. Dorsal surface of cranium relatively flat over neurocranium, sloping anteriorly to anterior terminus of nasals. Zygomatic arch deep; posterior extremity of jugal bears very small ectoglenoid process (Fig. 2a, d). Postorbital process of jugal distinct and pointed. Zygomatic process of squamosal arises well anterior of occiput. Very small postglenoid process forms posterior border of glenoid fossa, and curves slightly anteriorly at extremeity giving glenoid fossa a semicircular shape when viewed laterally (Fig. 2a, d). Auditory bullae highly inflated. Posterior parietal and occipitals not preserved.

Upper Incisors—Holotype I1 high crowned, arcuate when viewed laterally (Fig. 2a, b, d). I2 identical in crown height to I3. Stout I3 crown sub-triangular in buccal view (Fig. b). Occlusal surface oriented anteroposteriorly.

P3—Holotype sectorial anteroposteriorly elongate blade-like P3, bears seven buccal and lingual enamel ridgelets ascending anterodorsally from 7 main crest cuspules. Anterior third flexes slightly buccally, bears moderately well-developed posterolingual eminence. P3 much longer than all molars, but identical length to M1–2 combined (Fig. 2b).

Upper Molars—Bunolophodont. Holotype with M1 slightly worn, dentine of protocone, paracone and metaconule breached; M2 slightly worn, dentine of paracone breached; M3–4 unworn (Fig. 2b). M1 protoloph and metaloph of equal width. M2–4 protoloph wider than metaloph. Lingual margin of tooth row virtually straight, buccal margin convex laterally due to posterior size reduction of molars. Paracrista low but distinct, merges with weaker (worn) protocrista to form protoloph. Preprotocrista unites with preparacrista forming precingulum, postprotocrista weak, unites with a strong premetaconulecrista. Metacone higher crowned than metaconule. Metacrista well developed forming majority of metaloph, metaconulecrista weak. Premetacrista and postparacrista weakly developed and do not unite. Postmetacrista moderately well developed, terminates in position of stylar cusp E. Weak postmetaconulecrista joins postmetacrista at position of stylar cusp E defining posterior border. M4 highly reduced, protocone well-developed, paracone reduced, metacone highly reduced, metaconule absent.Preparacrista forms a small precingulum, paracrista weak, unites with well-developed preprotocrista. Postparacrista runs postero-buccally and contacts metacone defining posterior border of M4 (Fig. 2b).

Dentary—holotype left dentary complete, m4 absent. Right dentary articular process not preserved. Horizontal ramus stout with a convex ventral margin, digastric eminence deep, occurs below m1 hypolophid (depth 8.7 mm; Figs. 2e–j). Digastric sulcus shallow (Fig. 2e, j). Buccinator sulcus straight, shallow, occurs beneath posterior third of p3 to protolophid of m1. Anterior root of vertical ascending ramus adjacent to posterior of m3 protolophid (Fig. 2e, j). Angular process wide; lingual border thickened, tip pointed posteriorly. Masseteric fossa deep, ventral border extends well below buccinator sulcus to half depth of horizontal ramus. Anterior insertion area for second layer of masseter muscle thin and restricted to rim of masseteric fossa (Fig. 2e, j). Masseteric foramen large, anteroventrally oriented and leads into masseteric canal, which extends to beneath m1 protolophid. Mandibular foramen oval shaped, opening largely posteriorly (Fig. 2g, h). Articular process anteroposteriorly broad, articular condyle small, wider laterally. Coronoid processes anteroposteriorly broad (viewed laterally), with slight posterior ‘hook’ at dorsal end.

Lower Incisor—Holotype i1 lanceolate, bears moderate wear on anterior half of superior border (Fig. 2f, i). Diastimer short.

p3—Holotype p3 blade-like, anteroposteriorly elongate, straight within line of tooth row, unworn. Bears 8 buccal and lingual enamel ridges, which descend vertically from 8 crest cuspules. p3 much longer than all molars, but identical length to m1–2 combined (Fig. 2e–j).

Lower Molars—Bunolophodont. Holotype with m1 slightly worn, dentine of protoconid and hypoconid breached; m2 slightly worn, dentine of hypoconid breached; m3–4 unworn (Fig. 2f, i). Lophid faces smooth; m1 protolophid narrower than hypolophid, m2-4 hypolophid narrower than protolophid. Metaconid and entoconid higher crowned than protoconid and hypoconid. Pre- and post-metacristids and pre- and post-entocristids all well developed. Well-developed metacristid, forms protolophid, protocristid weak. Well-developed entocristid forms hypolophid, hypocristid weak. Low lingual cristid obliqua bisects interlophid valley. Paracristid (buccal) merges with premetacristid enclosing small trigonid basin. Small postcingulid defined by equally developed postentocristid and posthypocristid. Highly reduced m4, crown height of metaconid, protoconid and hypoconid subequal, entoconid absent. Weak premetacristid merges with buccal paracristid defining reduced trigonid basin. Weak buccal cristid oblique connects protolophid and hypolophid (Fig. 2f, i).

Comparison with other taxa

Cranium—Smaller than *B. penicillata*, *B. gaimardi*, *B. lesueur* and *B. tropica* but larger than *B. pusilla*. The skull of *Bettongia anhydra* (Table 1) can be distinguished from other bettongs by the following characters: The bunodont dentition is large relative to cranium size and includes a large, elongate P3; highly developed posterior molar gradient (M1 ≤ M2 > M3 >> M4); M4 highly reduced. The rostrum is anteroposteriorly compressed with strongly constricted frontals and exceptionally narrow nasals (Table 1) that constrict at the maxilla-pre-maxilla suture so that anteriorly, the left and right nasal suture and the nasal-premaxilla sutures are sub-parallel. The nasal-frontal sutures are arcuate (*sensu B. moyesi*) and extend posterior of the anterior edge of the orbit.

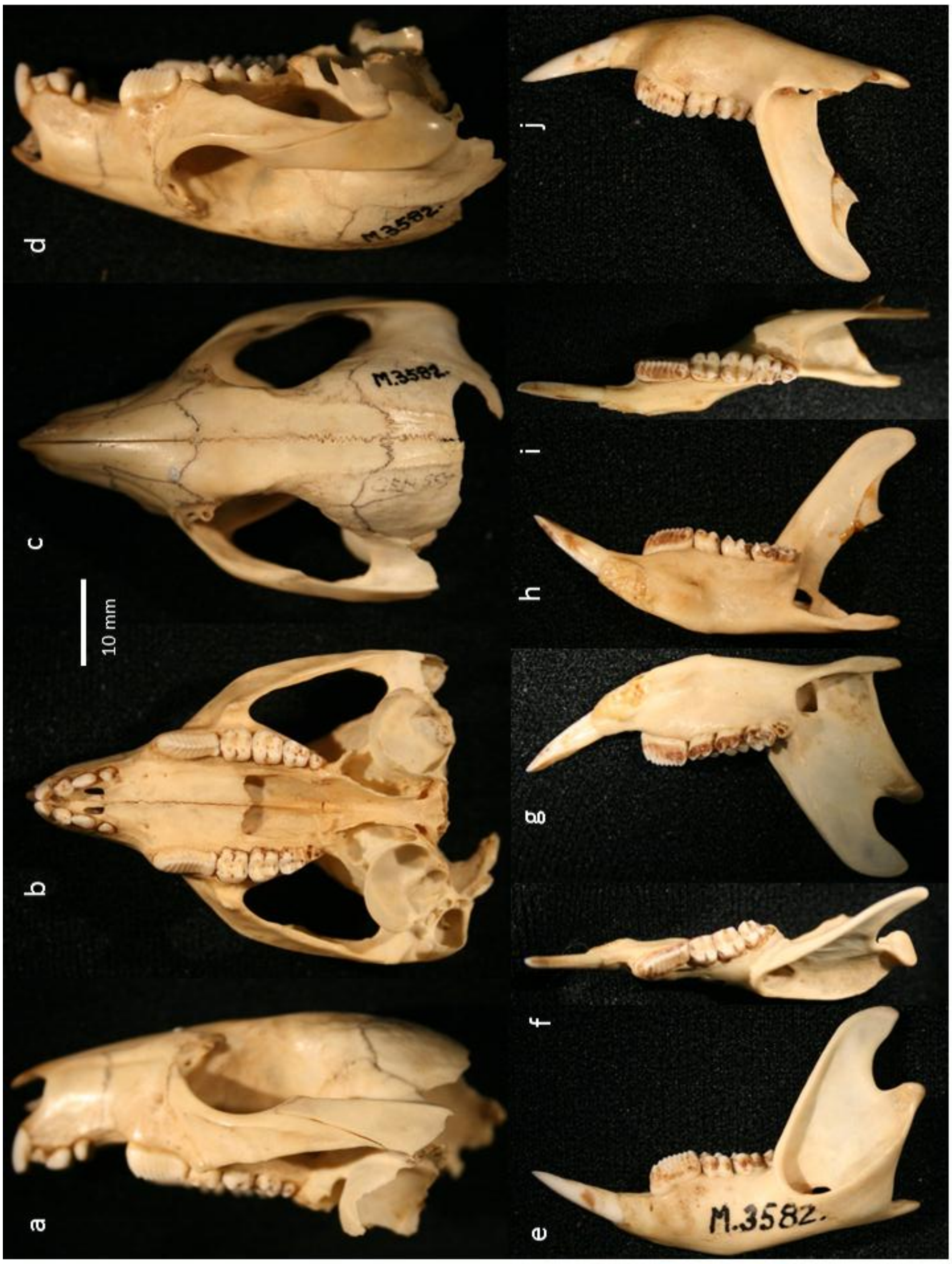

Fig. 2: The holotype (SAM M3582) of *Bettongia anhydra*. a. Left lateral, b. occlusal, c. dorsal aspect of skull; e. buccal, f. occlusal, g. lingual aspect of left dentary; h. buccal, i. occlusal, j. lingual aspect of left dentary aspect of left dentary

The interorbital constriction is more marked than in any other species in the genus (Table 1); the braincase is relatively narrow and more tapered anteriorly than in other bettongs (Finlayson 1958). The squamosal makes a large contribution to the zygomatic arch which is deep and robust. Differs from *B. penicillata*, *B. gaimardi* and *B. tropica* in the degree of inflation of the (incomplete) auditory bullae (Table 1), which are wide and deep and appear to be as highly inflated as the bullae of *B. lesueur*. The origin scars of the temporalis muscles are well developed, but unlike other bettongs (and *Aepyprymnus*), do not follow the interorbital ridge. Instead, they run diagonally across the anterior frontal then medially across the posterior frontal and parietal bones, suggesting relatively longer temporalis muscles (Finlayson 1958). The diastema and anterior palatal foramina are very short, the posterior terminus of the latter occurring near the anterior border of the canine. The posterior palatal foramina are large with anterior margins occurring near the posterior margin of M^1 but are short compared with other bettongs.

P3—The P3 of *B. anhydra* differs from *B. gaimardi*, *B. lesueur*, *B. moyesi*, *B. pusilla* and *B. tropica* in which P3 is straight and in line with the molar row, differs from *B. gaimardi*, *B. lesueur*, *B. moyesi* and *B. tropica* in which the lingual face of P3 is convex, differs from *B. penicillata* in which P3 flexes antero-buccally outside the line of the molar row (in *B. anhydra*, P3 flexes slightly antero-buccally, but remains within the line with the molar row); differs from *B. gaimardi*, *B. lesueur*, *B. pusilla* and *B. tropica* in which the superior and inferior borders of P3 are sub-parallel, but is similar to *B. penicillata* in that antero-buccal flexation of P3 increases the depth of the enamel on the anterior buccal face of the tooth such that it is approximately twice as deep as the posterior of the tooth (Wakefield 1967).

Table 1: Mean Cranial and dental measurements (mm) of modern Bettongia species. Data for *Bettongia gaimardi cuniculus*, *Bettongia gaimardi gaimardi*, *Bettongia penicillata ogilbyi* and *Bettongia tropica* from Wakefield (1976) and data for *Bettongia lesueur* from Finlayson (1958)

	Bettongia anhydra	*Bettongia gaimardi cuniculus*	*Bettongia gaimardi gaimardi*	*Bettongia lesueur*	*Bettongia penicillata ogilbyi*	*Bettongia tropica*
Basal Length	-	70.6	64.4	57.2	66.5	64.2
Zygomatic Width	37.4	45.3	42.2	43.0	24.2	41.2
Interorbital Width	12.2	19.9	18.5	14.5	17.4	15.8
Nasals Length	23.7	34.7	30.8	26.3	32.5	29.6
Nasals, Greatest Width	9.5	14.5	13.9	12.8	13.5	13.5
Rostrum Width	13.5	17.4	15.4	17.9	16	14.3
Nasal Opening Width	5.1	9.1	8.7	6.8	7.9	7.8
Bulla Length	10.4	12.5	12.1	15.9	14.2	13.8
Bulla Depth	-	9.5	9.1	-	10.6	10.9
P3 Length	7.5	8.1	7.2	8.5	7.3	8.3
M1-3 Length	10.5	**13.7**	12.8	11.7	12.4	13.2
M4 Length	1.4	3.8	3.3	2.5	2.6	2.8

Upper molars—Upper molars of *B. anhydra* differ from all other bettongs in the steepness of the molar gradient and extreme reduction of M4. It further differs from *B. pusilla* in which m1–4 approach equal size and have higher crowned, more lophodont molars (McNamara 1997); *B. gaimardi* in which M4 is only slightly smaller than M1–3 and in *B. penicillata*, *B. lesueur* and *B. tropica* in which M1 ≤ M2 > M3 > M4, but M4 is much less reduced.

Dentary—Dentaries of *B. anhydra* are short relative to tooth-row length and in lateral view the ascending ramus of *B. anhydra* obscures the view of m4 and most of m3. In *B. gaimardi*, *B. lesueur*, *B. penicillata* and *B. pusilla* the ascending ramus obscures the view of m4 only and in *B. moyesi* the ascending ramus obscures only part of m4. The dentary of *B. anhydra* also differs from *B. gaimardi, B. lesueur*, *B. penicillata* and *B. pusilla* in the robustness of the horizontal ramus (the ventral margin of the jaw of *B. moysei* is unknown), the greatest depth of which occurs quite anteriorly at the digastric eminence below m1 (Finlayson 1957, 1958). It differs from

B. penicillata, *B. gaimardi*, *B. moysei*, *B. pusilla* and *B. tropica* in the proportions of the coronoid process which is long and broad with sub-parallel borders, and in the angle between the ascending ramus and horizontal ramus which is more acute.

p3—p3 of *B. anhydra* has fewer, more broadly spaced cuspules and grooves than seen in *B. lesueur* and differs from *B. gaimardi*, *B. lesueur*, *B. moysei* and *B. tropica* in that the anterior portion of p3 deflects slightly buccally, though not as much as in *B. penicillata*; differs from *B. gaimardi*, *B. lesueur*, *B. pusilla* and *B. tropica* in which the superior and inferior borders of p3 are sub-parallel, but is similar to *B. penicillata* in that antero-buccal flexation of p3 increases the depth of the enamel on the anterior buccal face of the anterior portion of the tooth making it slightly deep than in the posterior portion of the tooth (Wakefield 1967).

Lower molars—Lower molars of *B. anhydra* can be distinguished from other bettongs by its high posterior molar gradient where m1 $\leq$ m2 > m3 >> m4 and the extreme reduction of m4 (as in upper molars).

Discussion

The tribes of Subfamily Potoroinae can be challenging to separate, particularly when presented with fragmentary fossil specimens. The lack of a dorsal (Flannery and Archer 1987) and ventral (Prideaux 1999) enamel flange on I_1 has been cited as a diagnostic feature of Tribe Bettongini. These characters appear to be quite variable and may be present on juveniles only. Fortunately there are several much less ambiguous characters (identified above) that can definitively separate tribes Bettongini and Potoroini. Therefore, we discourage the use of enamel flanges on I_1 to distinguish between the tribes.

Taxonomy

Finlayson (1957; 1958) stated that he would have erected *B. anhydra* as a distinct species had a series of specimens demonstrating the same distinctive characters existed. When represented by a single specimen only, it may have been reasonable for Wakefield (1967) to declare *B. p. anhydra* a synonym of *B. lesueur*. However, now a morphologically distinct, geographically widespread (Fig. 1) series of fossil specimens that occurred sympatrically with *B. lesueur* and *B. penicillata* have been located warranting the elevation of *B. anhydra* to specific level. Preliminary molecular evidence generated from a turbinal bone sampled from the holotype supports *B. anhydra* as a distinct species but further analysis is required before its taxonomic position can be confirmed.

Functional adaptations

Many of the differences between *B. anhydra* and other bettongs (reduced rostral length; shortened diastema, shortened anterior and posterior palatal foramina and reduction of the fourth molars) appear to be related to the shortening of the splanchnocranium and dentary. When occupying temperate parts of Australia, bettongs are primarily mycophagists. However, *B. lesueur*, the most arid adapted extant bettong, subsists mainly on roots and tubers. It also occasionally consumes bulbs, carrion, insects and seeds, including those of the Quondong and Sandalwood (*Santalum* spp.) which have hard seed-coats (Claridge *et al*. 2007). Studies of the cranial morphology of other mammals have identified the rostrum as one region of the cranium that reflects adaptive change, particularly associated with feeding, digging and changes in precipitation (e.g., Mora *et al*. 2003; Pergams and Lawler 2009; Wilson and Sánchez-Villagra 2010). By shortening the rostrum and dentary but retaining full sized anterior dentition, *B. anhydra* may have been able to apply greater bite force to its anterior dentition, potentially allowing it to exploit harder foods such as large seeds. The most striking characteristic that *B. lesueur*, and *B. anhydra* share is the extreme inflation of their auditory bullae. Desert dwelling mammals frequently develop inflated auditory bullae to improve low frequency hearing and predator detection, thereby allowing them to forage in more open areas (e.g., Francescoli *et al*. 2012). It is difficult to determine whether this characteristic indicate a close relationship or an independently derived adaptations to aridity. However, molecular phylogenetic analyses should resolve this question.

Ecological implications

Since Europeans colonised Australia all *Bettongia* spp. have either been extirpated from the majority of their range or driven to extinction. *B. gaimardi gaimardi* is now restricted to Tasmania and *B. gaimardi cuniculus* is probably extinct, *B. lesueur* is restricted to several small island of the western Australian coast, *B. penicillata ogilbyi* persists in a few small populations in southern Western Australia, *B. penicillata penicillata* is probably extinct and *B. tropica* persists in a small part of Queensland (see van Dyck and Strahan 2008). An extinct species, *B. pusilla*, is known exclusively from Holocene aged Nullarbor Plain cave accumulations. It is thought to have gone extinct sometime prior to European colonisation of Australia (McNamara 1997), but given the isolated nature of its known range, may have persisted until Europeans arrived. The recognition of *B. anhydra* further demonstrates how sensitive the genus is to habitat destruction and/or exotic predators and competitors.

The all-but-total loss of bettongs from Mainland Australia is likely to have had devastating ecological repercussions. Bettongs, potoroos and similar ground-foraging small mammals cultivate the soil and in doing so provide important eco-services. Soil disturbance has implications for incorporation of organic matter, aeration, improve moisture infiltration, seed germination and seedling establishment (Martin 2003). In addition, it promotes microorganism growth, influences topsoil formation and improves water penetration and retention, all of which enhance soil structure. Bettongs also play an integral role in the dispersal of seeds and fungal spores, many of which form symbiotic relationships crucial for the establishment and growth of many plants, particularly eucalypts (Claridge *et al*. 2007). These processes are so important that they may actually determine vegetation succession and lead to greater biodiversity (Martin 2003). The loss of Bettongs and other ground-foraging small mammals from much of mainland Australia may have compounded soil compaction problems caused by hard-hooved livestock, leaving little doubt that their loss will have enormous ecological impact (e. g., Johnson and McIlwee 1997; Garkaklis *et al*. 1998; Martin 2003).

Conclusion

Flannery and Archer (1987) considered *B. moyesi* to be the most plesiomorphic known species of *Bettongia*. They observed that it shares many plesiomorphic similarities with *B. lesueur* and suggested that the two species lie outside a clade containing the other extant species of *Bettongia*. We have shown that *Bettongia anhydra* is a distinct species that has more features in common with *B. lesueur* and *B. moyesi* than *B. gaimardi*, *B. penicillata* or *B. tropica*, though they may represent convergence rather than common ancestry. Molecular phylogenetic analyses are required to confirm the findings of this morphological analysis.

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Supplimentary information

Specimens used for comparison with *Bettongia anhydra*.

Bettongia gaimardi (Desmarest 1822): SAM M7386, M7387, M7388.

Bettongia lesueur (Quoy and Gaimard 1824): FUR 034 (Holocene fossils from Corra-Lynn Cave, Yorke Peninsula, South Australia); SAM M1702, M10769.

Bettongia penicillata (Gray 1837): FUR 011, 031;SAM M6211, M11247; WAM 66.1.7c, 66.12.11, 66.12.4a, 66.12.4b, 66.6.58, 67.10.193, 67.10.194, 67.10.31, 67.10.324, 67.10.360, 67.10.37, 67.10.523, 67.10.525, 67.3.54, 67.3.98, 67.5.1, 67.5.4, 67.5.41, 67.5.42, 7.5.43, 67.5.44, 67.8.69, 68.3.17, 69.7.649, 69.7.655, 69.7.661, 70.5.22, 70.5.23, 71.9.36, 72.1.109, 72.1.1104, 72.1.1105, 72.1.139, 72.1.199, 72.1.224, 72.1.467, 72.1.489a, 72.1.489b, 72.1.634a, 72.1.634b, 72.1.676, 72.1.776, 72.1.777, 72.1.778, 72.1.800, 72.1.824, 72.1.845, 72.1.846, 72.1.847, 72.1.898a, 72.1.898b, 72.1.924, 72.6. 184, 75.12.21, 76.4.35.

Bettongia pusilla McNamara 1997: SAM P35442, P35446, P35450, P35451; WAM 67.10. 227, 67.10.412, 68.3.5, 71.1.29a, 72.1.108, 72.1.822, 72.1.823, 76.10.413.

Bettongia tropica Wakefield 1967: MV C6870, AMNH 65279

CHAPTER 4

Natural Resource Management implications of the pre-European non-volant mammal fauna of the southern tip of Eyre Peninsula, South Australia

Context

This chapter documents the pre-European mammal fauna from the southern tip of Eyre Peninsula, a pseudo-island bound by the Southern Ocean to the south and aridity to the north. It provides data for comparison with the pre-European fauna of Kangaroo Island.

Statement of Authorship

I collected, prepared and analysed most of the material examined in this chapter (with additional support from those noted in the Acknowledgements). I supervised volunteers who assisted in specimen collection and preparation. I prepared the original and final manuscript for publication.

Graham C. Medlin also collect and helped prepare much of the material examined in this chapter, provided comments on the draft manuscript and contributed to the discussion.

Natural Resource Management implications of the pre-European non-volant mammal fauna of the southern tip of Eyre Peninsula, South Australia

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Abstract

Sinkholes and coastal caves located in, around and between the Coffin Bay and Lincoln National Parks were surveyed for pre-European fossils, which were collected from or just below the sediment surface. Twenty-four pre-European fossil samples, including eight already in the collections of the South Australian Museum, were analysed and 25 native and five introduced species of non-volant mammal were identified. Native and introduced species were often found together, indicating that the sites have accumulated mammal remains in both pre- and post-European times. Only four of the non-volant native mammals recovered are known to be extant in the study area today (*Lasiorhinus latifrons*, *Macropus fuliginosus*, *Cercartetus concinnus* and *Rattus fuscipes*). In contrast, 20 native species recorded have been extirpated and one (*Potorous platyops*) is now extinct. *Cercartetus concinnus* was recorded from only one of the fossil assemblages but is known to be widespread in the study area today. This may indicate recent vegetation change related to European land management practices and may have implications for natural resource management in the area.

Introduction

European colonisation of Australia has had major environmental repercussions resulting in significant changes to South Australia's species, ecosystems and landscapes, as well as forcing a decline in biodiversity. At least 23 mammal, 2 bird and 26 plant species have become extinct in South Australia since European settlement. Many European practices continue to threaten native species, resulting in the need for natural resource management (NRM) (DEH 2007; Morton *et al*. 2009). The number of threatened species and ecological communities is large and growing, but relatively few are being managed for recovery. Many of South Australia's ecosystems suffer from a suite of impacts including habitat modification, community and population fragmentation, invasive species and altered environmental water flows and fire regimes (DEH 2007). Although much has been done to limit further ecosystem degradation, additional capacity, knowledge and time is needed to protect, conserve, and rebuild them (DEH 2007). Ecosystem restoration is fundamental to NRM, but in order to make informed decisions, we must first research and understand the pre-European distribution of native taxa.

Efforts have been made to determine the pre-European vertebrate fauna for various regions of Australia. Much of this work has been carried out in Western Australia and the Nullarbor Plain (Baynes 1984, 1987; Morton and Baynes 1985), south-eastern Australia (Wakefield 1972 [and papers cited therein]; McDowell 2001), Flinders Ranges (Smith 1977; Medlin 1993) and parts of central Australia (Baynes and Baird 1992; Copley *et al*. 1989; Baynes and Johnson 1996). Between the investigated areas lies Eyre Peninsula, an important bioregion of southern Australia. Eyre Peninsula has long been considered a faunal corridor between east and west (Baynes 1987), suggesting that the pre-European fauna of northern Eyre Peninsula should be composed of a mixture of western and eastern dwelling species

(Watts and Ling 1985). In addition, genetic relationships between populations of the bush rat (*Rattus fuscipes*) suggest that Eyre Peninsula may once have been a corridor to Kangaroo Island (Hinten *et al*. 2003). However, for all of its importance, relatively little is known of Eyre Peninsula's pre-European fauna. Only two Quaternary fossil sites have been reported from northern Eyre Peninsula (Venus Bay: Medlin 1996; McDowell 1997, and Darke Peak: Watts and Ling 1985; Baynes 1987), and only a single fossil site has been reported from southern Eyre Peninsula (South Block Range: Watts and Ling 1985; Baynes 1987).

In this study we surveyed sinkholes and rocky overhangs on the southern tip of Eyre Peninsula for pre-European fossil deposits that could be used to investigate the regions' pre-European non-volant mammalian fauna. This research developed ecological knowledge that has implications for natural resource management.

Materials and method

Study area

The southern tip of Eyre Peninsula (Fig. 1), which encompasses Coffin Bay National Park (CBNP), Lincoln National Park (LNP) and the Southern Basin Prescribed Wells Area (SBPWA), experiences a Mediterranean climate that is strongly influenced by south-westerly frontal systems. The region experiences an annual rainfall of approximately 500 mm, most of which falls during the winter months (DEH 2004a, b). Southern Eyre Peninsula is characterised by shallow, relatively infertile, calcareous soils with extensive sand dune formations near the coast (DEH 2004a). Much of the study area has been subjected to varying degrees of clearing, grazing, cropping, and the creation of 4WD tracks used for commercial and recreational access (Dennis 1994).

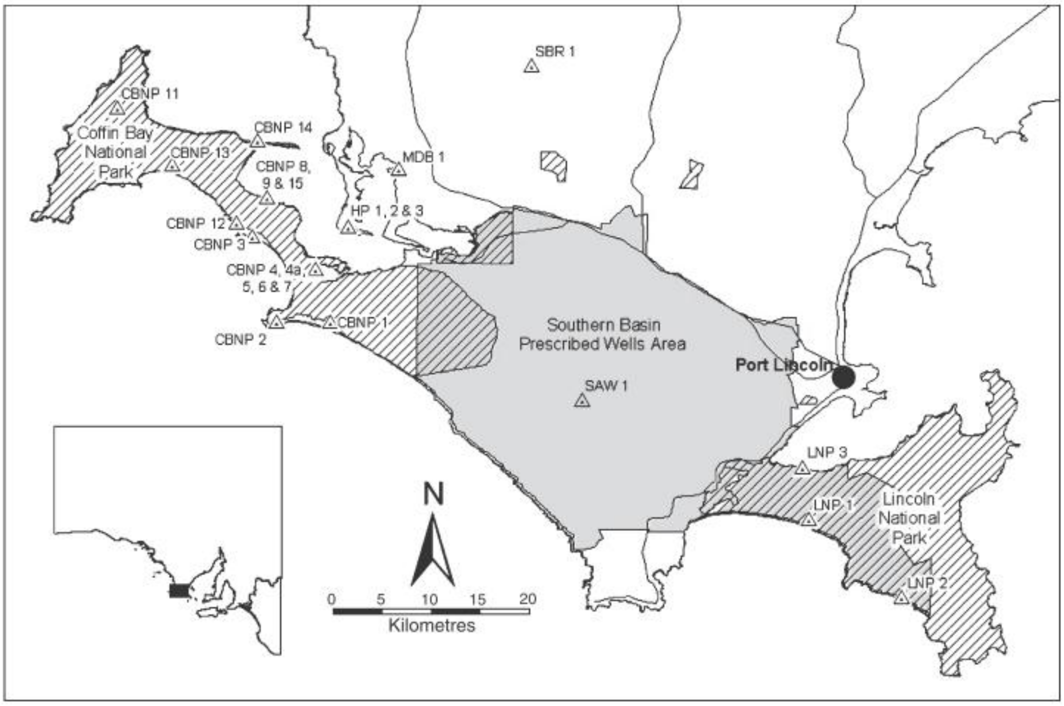

Fig. 1: Location of pre-European fossil accumulations on the tip of southern Eyre Peninsula. Triangles = Holocene fossil site, CBNP = Coffin Bay National Park, HP = Horse Peninsula, MDB = Mount Dutton Bay, SBR = South Block Range, SAW = SA Water (Southern Basin Prescribed Wells Area) and LNP = Lincoln National Park. Shading = Southern Basin Prescribed Wells Area and hatching = conservation area.

The vegetation of CBNP consists largely of coastal daisy-bush (*Olearia axillaris*) and coastal bearded-heath (*Leucopogon parviflorus*) open heath, but also contains large areas of drooping sheoak (*Allocasuarina verticillata*) and dryland tea-tree (*Melaleuca lanceolata*) open woodland and coastal white mallee (*Eucalyptus diversifolia*) open scrub. Extensive areas of bare sand dune blowouts also occur (Dennis 1994; DEH 2004a). The vegetation of LNP consists mainly of drooping sheoak and dryland tea-tree open woodland and a mallee complex that includes *Eucalyptus diversifolia* and ridge-fruited mallee (*Eucalyptus incrassata*) (DEH 2004b; Dennis 1994). The vegetation of SBPWA which occurs between the two parks consists mainly of mixed drooping sheoak and dryland tea-tree woodland with large areas of mallee (Dennis 1994). Before European colonisation, the vegetation of the study area is thought to have consisted primarily of sheoak grassy woodland

(Crocker 1946; Peeters *et al.* 2006), which was considered to be the most widespread vegetation association on Eyre Peninsula. However, since European settlement this vegetation association has undergone a drastic decline (Bishop and Venning 1986).

Collection and analysis

Fossils were collected from shallow, small diameter karst features (approx. 300 mm diameter and 900 mm depth), sinkholes and coastal caves, the sediment floors of which were exposed to the elements. Each accumulation was allocated a unique alpha-numeric code that described the location and order of discovery; however, local names were also recorded. Where possible surface sediments were excavated and sieved through 2 mm mesh to concentrate fossils. Where sieving was not possible, fossils were handpicked from floor of the karst features. Concentrated samples were sorted using a cardboard tray to expose diagnostic bones, which were picked out with forceps and placed in labelled containers. Diagnostic bones (whole and part skulls, dentaries and/or teeth) were identified using published descriptions and comparative material held by the South Australian Museum (SAM). All specimens were identified to the lowest taxonomic level possible (usually species). Dingos and domestic dogs (*Canis lupus familiaris/dingo*) were treated as morphological equivalents. All specimens were deposited in the SAM Mammal Section's Subfossil Collection.

Results

Fossils from 16 new sites, combined with eight pre-existing South Australian Museum samples were analysed. The remains of 30 species of non-volant mammal (including 5 introduced species) were recovered from lower Eyre Peninsula. These included 5 carnivorous marsupials, 2 bettongs, an extinct potoroo, 2 macropodids, 3 bandicoots, 2 possums, a pygmy-possum, a wombat, and 8 native rodents (Table 1).

The samples analysed provide positive data of the presence of the reported species either prior to, or after European colonisation. Different circumstances presented by different sites dictated how the samples were collected. Samples from sites CBNP 9, SBR 1 and SAW 1 were collected by excavating and sieving karst feature sediments. Samples from sites CBNP 4, CBNP 4a, CBNP 5, CBNP 6, CBNP 7, CBNP 8, CBNP 11, HP 1, HP 2, HP 3, LNP 2 and MDB 1 were collected by hand picking specimens from the floor of karst features. Samples from sites CBNP 1, CBNP 2, LNP 1 and LNP 3 were collected from the ground surface by DEH staff or park visitors. Samples from CBNP 3, CBNP 12 and CBNP 13 were collected from sand dune blowouts by DEH staff. Unfortunately, it is not known how samples CBNP 14 and CBNP 15 were collected.

Discussion

Modes of accumulation

Fossil samples recovered from sites CBNP9, SBR 1, SAW 1 and LNP 2 are consistent with nocturnal raptor accumulations (see Andrews 1990), though pitfall trapping probably contributed to the collection of large animals in SAW 1. Fossil assemblages from sites CBNP 3, CBNP 12 and CBNP 13 were collected from dune blowouts and may have been derived from Aboriginal middens. Fossil assemblages from sites CBNP 4, CBNP 4a, CBNP 5, CBNP 6, CBNP 7, CBNP 8, CBNP 11, HP1, HP2, HP3 and MDB 1 appear to have accumulated by pitfall trapping and/or autochthonous accumulation (see Baird 1991). Each of these modes of accumulation bias the sample they collect in different ways. Sites that have been collected by the same accumulation agent are comparable, but it is difficult to make direct comparison of species relative abundance from sites with different accumulation agents. However, presence data that shows that a species once occurred in a given area is useful for the assessment of species distribution and NRM issues.

Age of accumulations

None of the fossil accumulations have been radiometrically dated. However, exotic species have been recorded in half of the samples indicating that some of the collection processes were still operating after European colonisation. In addition, none of the mammals recorded became extinct until after European occupation. Therefore, it is likely that the fossils are of Holocene age. One possible exception may be the sample from South Block Range (SBR 1). This sample contains four species that are not recorded in any other sample (see Table 1) which may indicate that SBR 1 is an older accumulation, but is more likely due to its large sample size.

Table 1: (opposite) Mammals recovered from Holocene fossil deposits found on Southern Eyre Peninsula. CBNP = Coffin Bay National Park, HP = Horse Peninsula, MDB = Mount Dutton Bay, SBR = South Block Range, SAW = SA Water (Southern Basin Prescribed Wells Area) and LNP = Lincoln National Park. † = a pre-existing SAM collections, * = introduced species. CBNP10 was omitted because it did not contain mammal remains. The mammals recorded in SBR 1 have been modified from Watts and Ling (1985) and Baynes (1987). S = Small sample (unable to be sieved, all visible specimens hand picked from surface). M = Medium sample (5–15 L of surface sediments sieved). L = Large sample (15–30 L of surface sediments sieved).

	Sites																								
	CBNP 1†	CBNP 2†	CBNP 3†	CBNP 4	CBNP 4a	CBNP 5	CBNP 6	CBNP 7	CBNP 8	CBNP 9	CBNP 11	CBNP 12†	CBNP 13†	CBNP 14†	CBNP 15†	HP 1	HP 2	HP 3	MDB 1	SBR 1†	SAW 1	LNP 1	LNP 2	LNP 3	No. Sites
Sample size	S	S	M	M	S	S	S	S	S	M	S	S	S	S	S	S	S	S	M	L	L	S	S	S	
Dasycercus sp. indet.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	X	–	–	–	–	1
Dasyurus geoffroii	–	–	X	–	–	–	–	–	–	–	–	–	–	–	X	–	–	–	–	X	X	–	–	–	4
Parantechinus apicalis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	X	–	–	–	–	1
Sminthopsis dolichura	–	–	–	–	–	–	–	–	–	X	–	–	–	–	–	–	–	–	–	X	X	–	–	–	3
Sminthopsis griseoventer	–	–	–	–	–	–	–	–	–	X	–	–	–	–	–	–	–	–	–	X	X	–	–	–	3
Isoodon obesulus	–	X	X	–	–	–	–	–	–	X	–	–	X	–	–	–	–	–	–	X	X	–	–	–	6
Perameles bougainville	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	X	X	X	–	–	–	3
Macrotis lagotis	–	–	–	–	–	–	–	–	–	X	–	X	–	–	–	–	–	–	–	–	–	–	–	–	2
Lasiorhinus latifrons	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	X	–	–	–	1
Trichosurus vulpecula	–	–	X	X	–	–	X	X	–	X	X	–	–	–	–	–	–	–	X	–	X	–	–	X	9
Bettongia lesueur	–	–	X	X	–	X	–	X	–	X	–	–	–	–	–	–	–	–	X	–	X	–	–	–	7
Bettongia penicillata	–	–	X	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	X	–	X	–	–	–	3
Potorous platyops	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	X	X	–	–	–	2
Macropus eugenii	–	–	X	X	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	X	X	–	–	4
Macropus fuliginosus	–	X	–	–	–	–	–	–	X	–	X	–	–	–	–	–	–	X	X	–	X	–	–	–	6
Cercartetus concinnus	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	X	–	–	–	–	1
Pseudocheirus sp. indet.	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	X	–	–	–	1
Notomys mitchellii	–	–	X	–	–	–	–	–	–	X	–	–	–	X	–	–	–	–	–	X	X	–	–	–	5
Pseudomys australis	–	–	–	–	–	–	–	–	–	X	–	–	–	X	–	–	–	–	–	X	X	–	–	–	4
Pseudomys bolami	–	–	–	–	–	–	–	–	–	X	–	–	–	X	–	–	–	–	–	X	–	–	X	–	4
Pseudomys gouldii	–	–	–	–	–	–	–	–	–	–	–	–	–	X	–	–	–	–	–	–	–	–	–	–	1
Pseudomys occidentalis	–	–	–	–	–	–	–	–	–	X	–	–	–	X	–	–	–	–	–	X	X	–	–	–	4
Pseudomys shortridgei	–	–	–	–	–	–	–	–	–	X	–	–	–	–	–	–	–	–	–	X	X	–	–	–	3
Rattus fuscipes	–	–	X	X	–	–	–	–	–	X	–	–	X	X	–	–	–	–	–	X	X	–	X	–	8
Rattus tunneyi	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	X	–	–	–	–	1
*Oryctolagus cuniculus**	X	X	–	X	–	–	–	–	–	X	X	–	–	X	–	X	X	–	X	–	X	–	X	–	11
*Canis lupus familiaris/dingo**	–	–	–	X	–	–	–	–	–	–	–	–	–	–	–	–	–	–	X	–	X	–	–	–	3
*Vulpes vulpes**	–	–	–	X	–	–	–	–	–	X	–	–	–	–	–	X	–	–	–	–	X	–	–	–	4
*Felis catus**	–	–	–	–	X	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1
*Ovis aries**	–	–	–	X	–	–	–	–	–	–	–	–	–	–	–	–	–	–	X	–	X	–	–	–	3
No. Species	1	3	8	8	1	1	1	2	1	14	3	1	2	7	1	2	1	1	8	16	22	1	3	1	–

Species determinations

Mammal remains from the South Block Range site (SBR 1) have been previously reported by Watts and Ling (1985) and Baynes (1987). Some of the identifications made in these reports have been changed in this work. Specimens described by Watts and Ling (1985) and Baynes (1987) as *Sminthopsis* sp. murina group have been reassigned as either the little long-tailed dunnart (*S. dolichura*) or the grey-bellied dunnart (*S. griseoventer*) based on characteristics described by Kitchener *et al*. (1984) and SAM comparative specimens.

Watts and Ling (1985) and Baynes (1987) reported the sandy inland mouse (*Pseudomys hermannsburgensis*) from the SBR 1 sample. We believe that these specimens are more appropriately identified as Bolam's mouse (*P. bolami*). The first

upper molars of these two (similar) species differ in the shape of the occlusal surface of T1 (the lingual-most cusp of the first loph). The T1 of *P. bolami* has a circular or rounded occlusal surface whereas the T1 of *P. hermannsburgensis* has a much more anteroposteriorly elongate occlusal surface. These characteristics become more obvious with increased tooth wear. It is important to distinguish between these two species as though they are similar in appearance; they have quite different ecological needs. *P. hermannsburgensis* prefers hummock and tussock grasslands and stabilised sand dunes and fields (Breed 2008), whereas *P. bolami* is most commonly associated with chenopod shrubland or Acacia and Eucalyptus woodlands with loamy, clay or calcareous soils (Moseby and Read 2008).

Watts and Ling (1985) erroneously reported both the Shark Bay mouse (*P. fieldi*) and Gould's mouse (*P. gouldii*) from Eyre Peninsula. It has long been considered that these two taxa (along with *P. praeconis*, formerly the Shark Bay mouse, which Baynes (1990) synonymised with *P. fieldi*) are closely related and are potentially conspecific (Baynes 1979; Baynes 1990; Morris 2000). Baynes (1979, p. 313) stated his belief that “*Pseudomys gouldii* and *P. praeconis* are one species”. The authors are not aware of any morphological characteristics that can be used to differentiate skulls of *P. fieldi* from *P. gouldii*, which now appear to have a continuous fossil distribution from Western Australia to New South Wales (unpublished data). Genetic research is required to determine the status of these species, but if they are conspecific, taxonomic precedent requires use of the name *Pseudomys gouldii* Waterhouse 1839. Therefore, we refer to this morpho-species as *P. gouldii*.

Woolley (2005; 2006) states that the genus *Dasycercus* is made up of two species, the crest-tailed mulgara (*D. cristicauda*) and the brush-tailed mulgara (*D. blythi*), that are distinguishable genetically, on their tail forms, on the number of nipples in females and on the number of upper premolar teeth (three in *D. cristicauda* with no diastema and two in *D. blythi* with a diastema between P^2 and M^1). However, Masters (2008) reports that the P^3 found in *D. cristicauda* is “sometimes present on one side only”. Baynes (1987) identified two left *Dasycercus* maxillae found in the SBR 1 sample as *D. cristicauda*. The authors observed that one of the SBR 1 specimens had a large alveolus for a single rooted P^3 and lacked a diastema, whereas the other specimen had only two premolars but also lacked a diastema. Woolley (2005) reports three aberrant specimens from the SAM mammal collection. One specimen identified as *D. blythi* based on tail form that had a P^3 and two specimens identified as *D. cristicauda* based on tail form which lacked a P^3. Deciduous premolar teeth and unerupted permanent premolars may add to the difficulty of separating skeletal remains of the two species of *Dasycercus*. The presence of a third upper premolar appears to be definitive for *D. cristicauda*, but its absence may not be definitive of *D. blythi*. The presence or absence of a third premolar appears to be a variable character and may not be useful for separating skeletal remains of the two species without corroboration with genetic or tail characters. Consequently, specimens from SBR 1 could be diagnosed to genus only (*Dasycercus* sp. indet.).

This research is the first to report *Pseudocheirus* from Eyre Peninsula. Unfortunately, the identity of the species is unclear. The specimens collected may represent the common ringtail possum (*P. peregrinus*) or the western ringtail possum (*P. occidentalis*). Specimens of *P. occidentalis* were not available for comparison and the authors are not aware of any skeletal morphological characteristics that can be used to differentiate the two species. Therefore, the species is presented here as *Pseudocheirus* sp. indet. Baynes (1987) reported *P. peregrinus* from the south-western edge of the Nullarbor, but the subsequent recognition of *P. occidentalis* as a unique species suggests that these species determinations should be re-evaluated. The discovery of *Pseudocheirus* on Eyre Peninsula provides support for the concept that Eyre Peninsula has acted as an east-west biogeographic corridor.

Fauna

The fossil remains identified in this study suggest that the diversity of the pre-European fauna of the southern tip of Eyre Peninsula was comparable with mammalian diversity presented in other studies (e.g. Watts and Ling 1985; Baynes 1987; Copley *et al*. 1989). What is remarkable is just how depauperate the remaining native mammals have become since European settlement. The present mammal fauna of the southern tip of Eyre Peninsula are dominated by exotic species (Table 2). Small mammals, particularly rodents and small dayurids, occurred in many of the samples suggesting that they were widespread, but are almost nonexistent today. Similarly, medium-sized mammals, including burrowing bettongs (*Bettongia lesueur*), woylies (*B. Penicillata*), common brushtail possums (*Trichosurus* *vulpecula*), southern brown bandicoots (*Isoodon obesulus*) and western barred bandicoots (*Perameles bougainville*), also occur in many of the samples suggesting that they too were a successful part of the mammal community. However, they now appear to be totally absent from the present-day fauna. Apparently habitat loss, particularly in understorey vegetation, due to European land management practices and pressure imposed by exotic predators has had a devastating impact on the pre-European mammals that once occupied the study area.

Table 2: Modern terrestrial mammals recorded in the study area. C = Species reported in the 'Parks of the Coffin Bay Area Management Plan' (DEH 2004a). L = Species reported in the 'Lincoln National Park Management Plan' (DEH 2004b). V = Species reported in 'A List of the vertebrates of South Australia' (Robinson *et al.* 2000) * = introduced species. Records from Watts and Ling (1985) were omitted as they apply to the whole of Eyre Peninsula.

Species	Source
Lasiorhinus latifrons	V
Macropus fuliginosus	L
Cercartetus concinnus	L
Rattus fuscipes	V
*Rattus rattus**	V
*Mus musculus**	C, V
*Oryctolagus cuniculus**	C, L, V
*Canis lupus familiaris/dingo**	C, V
*Vulpes vulpes**	C, L
*Felis catus**	C, L
*Equus caballus**	C, L, V
*Bos taurus**	C

Despite being widespread and abundant in the study area today (Watts and Ling 1985; Robinson *et al*. 2000), the house mouse (*Mus musculus*) is absent from all of the sites sampled. *M. musculus* is most often collected by owls. This suggests that owls vacated the study area before the arrival of *M. musculus*, possibly due to the extirpation of their small native mammal food source, and never returned to the cave roost sites sampled. Owls still occur in the study area today, but probably occupy tree roosts where they are safer from exotic predators. All other exotic species have been collected by natural pitfalls, which *M. musculus* may be able to avoid.

Three small diameter (200–300 mm), shallow (900mm) sinkholes (CBNP 5, CBNP 6 and CBNP 7) were found to contain several *T. vulpecula* and/or *Bettongia* spp. skulls from which they could have easily escaped if alive. This suggests that the karst features may have been used as shelters or nest sites and further implies that while there must have been adequate underbrush to provide shelter for *Bettongia* spp. and Peramelids, there may not have been an adequate supply of tree hollows (characteristic of tall eucalypts) that could be used by *T. vulpecula* for shelter and nesting. This supports Crocker's (1946) assessment that the dominant vegetation of lower Eyre Peninsula was sheoak woodlands with a thick grassy/shrubby understorey.

DEH (2004a, b) reported the western grey kangaroo (*Macropus fuliginosus*), *R. fuscipes* and western pygmy-possum (*Cercartetus concinnus*) as extant in the study area (see Table 2). In addition, Robinson *et al*. (2000) indicate that the hairy-nosed wombat (*Lasiorhinus latifrons*) also occurs in the study area (the authors observed an active wombat burrow and scats presumed to be made by *L. latifrons* at Mount Dutton Bay near site MDB1). Each of these species occurred in the fossil record, but were not represented equally. Small mammals, including *R. fuscipes*, several species of native false mice (*Pseudomys* spp.), Mitchell's hopping mouse (*Notomys mitchellii*) *T. vulpecula*, *Bettongia* spp., *I. obesulus*, *P. bougainville* and rabbits (*Oryctolagus cuniculus*), occur in several of the surveyed sites (Table 1) and *R. fuscipes* appear to have been the most widespread native mammal in the study area (Watts and Ling 1985; DEH 2004a, b). This may be caused by collection mode bias, reflecting the dietary preferences of owls and humans, but probably also reflects past population density. Small numbers of *M. fuliginosus* remains occurred in several of the sinkholes suggesting a low population density, though this may simply reflect the relatively small diameter of sinkholes surveyed. By contrast, *C. concinnus*, which is common in the national parks of southern Eyre Peninsula at present, was recovered from the South Block Range site only. Hand picking specimens from surface sediments may have biased the fossil assemblages to exclude smaller species such as *C. concinnus*. However, it is possible that *C. concinnus* did not occur in the more southern parts of the study area where drooping sheoaks are thought to have been dominant prior to European colonisation (Crocker 1946; Bishop and Venning 1986; Peeters *et al.* 2006). More research is needed to determine the significance of the apparent absence of pygmy-possums from the majority of accumulations.

Three other species, *Dasycercus* sp. indet., the dibbler (*Parantechinus apicalis*) and the pale field-rat (*Rattus tunneyi*) were also restricted to SBR 1, and all share a preference for sandy substrates (Aplin *et al*. 2008; Masters 2008; Woolley 2008). This site may be older than the more southerly fossil locations, but is much further from the coast than all of the other sites and as a result may experience greater aridity. This probably explains the presence of *Dasycercus* sp. indet. in the SBR 1 sample, and its absence from the other more coastal sites as both species of *Dasycercus* have largely arid zone ranges (Woolley 2005; 2006). It may also explain the fossil distribution of *P. apicalis*, but little is known of the ecology of this species. *Rattus tunneyi* prefers tall grassland and burrows in loose sandy soil (Aplin *et al*. 2008). Baynes (1979; 1982) reported that *R. tunneyi* had a preference for calcareous (rather than quartz) sand substrates such as the mobile sand dunes that built up in the south of Western Australia during the Holocene. Coastal dunes and extensive dune blowouts occur frequently on the southern tip of Eyre Peninsula. However, the absence of *R. tunneyi* from all of the southern sites suggests that dunes blowouts were not available as habitat for *R. tunneyi* prior to European settlement. This suggests that they were formed after European settlement, probably as a result of vegetation degradation. This scenario supports the interpretation of a restricted fossil distribution of *C. concinnus* and suggests that European land clearance and high grazing pressure has modified the natural vegetation of the southern tip of Eyre Peninsula, which allowed *C. concinnus* to extend its range further south.

The rich pre-European fauna recorded from southern Eyre Peninsula indicates strong potential for translocation of several extirpated native mammals. However, success would probably depend on the control of exotic species such as dogs, foxes, cats, rabbits and horses, but also impact-causing native species such as *M. fuliginosus*, which apply high grazing pressure on remnant native vegetation (DEH 2004a, b).

This study provides an initial synopsis of the composition and distribution of the pre-European mammal fauna of the southern tip of Eyre Peninsula and provides data that should be considered when making NRM decisions. However, further research is required to verify the findings of this research and improve our understanding of the area's pre-European community composition. Further research is also needed to investigate the pre-European range of the *C. concinnus* and *R. tunneyi* on southern Eyre Peninsula. In addition, more stratified Holocene fossil accumulations must be located, excavated and radiometrically dated to investigate trends in the diversity and abundance of lower Eyre Peninsula's pre-European mammal fauna as well as the environmental trends that drove them.

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CHAPTER 5

The impact of European colonization on the late Holocene non-volant mammals of Yorke Peninsula, South Australia

Context

This chapter documents the per-European mammal fauna from the southern part of Yorke Peninsula, a pseudo-island bound by the Southern Ocean to the south and aridity to the north. It provides data for comparison with the pre-European fauna of Kangaroo Island.

Statement of Authorship

I collected some of the material and prepared, identified and analysed most of the material examined in this chapter (with additional support from those noted in the Acknowledgements). I supervised volunteers who assisted in specimen preparation. I prepared the original and final manuscript for publication.

Alexander Baynes provided preliminary identifications of specimens from one of the assemblages collected in the 1980's, commented on the draft manuscript and contributed to the discussion.

Graham C. Medlin provided advice on specimen identification, commented on the draft manuscript and contributed to the discussion.

Gavin J. Prideaux provided guidance and advice, commented on the draft manuscript and contributed to the discussion.

The impact of European colonization on the late Holocene non-volant mammals of Yorke Peninsula, South Australia

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Abstract

Over the last 200 years Australia has suffered the highest rate of species extinctions of any continent. This demands extensive biodiversity research, but unfortunately has been hampered by poor documentation of Australia's native species at the time of European colonization. Late Holocene fossil assemblages preserved in caves, rockshelters and surface lag deposits from deflated sand dunes can provide a more complete understanding of pre-European ecological conditions than can be developed from our knowledge of present biodiversity. In South Australia, few regions have experienced greater landscape modification and biodiversity loss than Yorke Peninsula. We investigate the composition, richness, evenness and age of two owl accumulations from southeastern and southwestern Yorke Peninsula and contrast them with a surface lag deposit assemblage probably accumulated by humans. We then examine the pre-European biogeography of the fauna recovered. The three assemblages have similar species richness, but differ dramatically in composition and evenness. The biases imposed by differing accumulation agents can explain compositional differences between owl and human assemblages, but not the differences between the respective owl accumulations. We argue that key substrate differences — one area is dominated by sand and the other by calcrete — have favoured distinct vegetation communities that fostered distinctly different mammal assemblages from which raptors accumulated prey. The ecological requirements of the extant mammals appear to be reflected in the fossil assemblages, providing support for the concept of uniformitarianism and confidence in the relevance of late Holocene fossil assemblages to modern conservation and natural resource management.

key words: Palaeoecology European impact, extinction, climate change, small mammal, biogeography late Holocene, Australia.

Introduction

European colonization has had major environmental repercussions that have fundamentally transformed Australia’s species, ecosystems and landscapes, causing widespread declines in biodiversity (e.g. Bickford and Gell 2005; McDowell and Medlin 2010). Faced with environmental change, organisms may remain unaffected, or may respond with dispersal, population size or density change, clinal shift, evolution, extirpation or extinction (Hadly 1996; Barnosky and Bell 2003; Barnosky 2008). Therefore, it is of fundamental importance for natural resource management that we understand the impacts of past environmental change as a key to predicting and preparing for future changes in biodiversity. Such predictions rely on a detailed understanding of the impacts of past environmental variation, yet few datasets used in biodiversity assessments span more than one full generation of the targeted organism (Willis *et al.* 2005; Willis *et al*. 2007; Froyd and Willis 2008). When historical records lack adequate temporal depth, conservation, natural resource and landscape managers can turn to the Holocene palaeoecological record to develop a better understanding of the ecology of extant organisms and their response to past environmental changes (Birks 1996; Lyman 1996; Delcourt and Delcourt 1998; Swetnam *et al*. 1999; Jackson and Erwin 2006; Froyd and Willis 2008). Species composition, diversity, relative abundance, richness and evenness of Holocene fossil assemblages can be compared with those of modern ecosystems to assess the degree of modification or degradation that an ecosystem has experienced (Hadly and Barnosky 2009).

Holocene fossil deposits usually consist of unstratified surficial raptor assemblages and lag deposits (e.g., dune blowouts). Due to the dynamic nature of such settings, they are typically assumed to be geologically very young. It might even be argued that the age of such accumulations is not relevant due to the high potential for time averaging, a taphonomic process whereby specimens accumulated at different times becoming mixed together. Some researchers (Hadly 1999; Barnosky *et al*. 2003; Barnosky and Shabel 2005) have suggested that due to an increased potential for the inclusion of rare taxa, time averaging may actually be beneficial under these circumstances. However, with no knowledge of the extent of time that has elapsed over the depositional period, this concept is difficult to assess. Further, without radiometric dating, comparison between fossil accumulations erroneously assumed to be of similar age may be invalid.

In Australia to date efforts have been made to determine the pre-European vertebrate fauna for various regions (e.g., Wakefield 1972; Baynes 1984, 1987; Morton and Baynes 1985; Copley *et al.* 1989; Baynes and Baird 1992; Medlin 1993; Baynes and Johnson 1996; ; Baynes and McDowell 2010; Start *et al*. 2012), but only one study of a late Holocene mammal assemblage (McDowell 1997) has investigated paleoecological change within a tight chronological framework.

No region of South Australia has been more impacted by European colonization than Yorke Peninsula (Figure 1). Due to its gentle topography and relatively predictable climate, Yorke Peninsula has been subjected to extensive vegetation clearance for agriculture, habitat modification, introduction of invasive species, and altered environmental water flows and fire regimes (Department for Environment and Heritage [DEH] 2007). Consequently, little is known of the pre-European mammalian fauna. Recent biological surveys (Neagle 2008) have provided information about Yorke Peninsula's current biodiversity, but the potential of the Holocene fossil record remains untapped. This study seeks to test key assumptions frequently made about Holocene fossil deposits, which include their age, the effects of time averaging, their utility for determining species distribution baselines and the validity of uniformitarianism. We use AMS radiocarbon dating to assess the age and extent of time averaging, and analyze composition, relative abundance, richness and evenness of mammal species in two large unstratified owl accumulations (INPA and TRHA, Figure 1) and one surface lag deposit (BALA, Figure 1). The assemblages are compared and contrasted to assess their relevance to natural resource and conservation management and the degree of time averaging they have experienced.

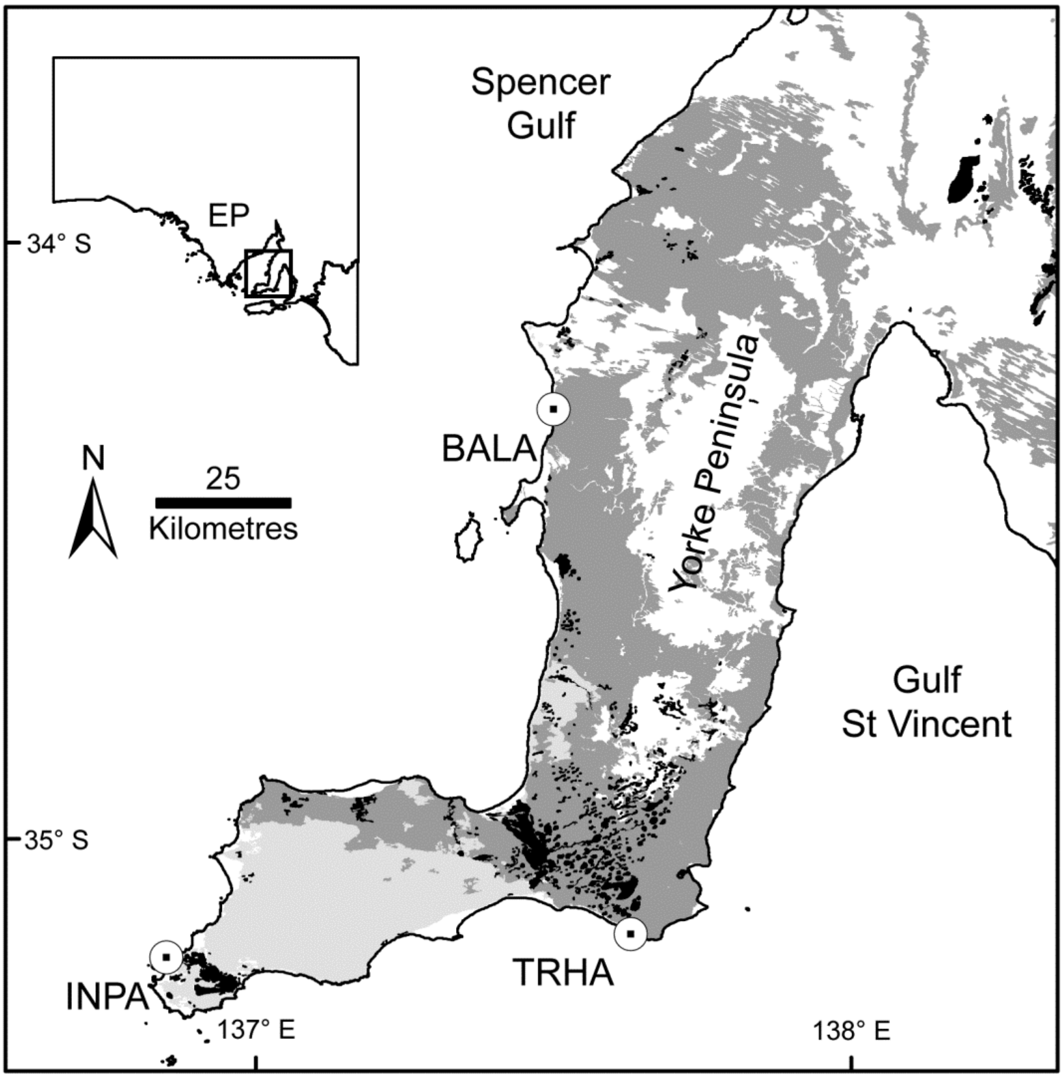

Figure 1. Location of fossil assemblages, pre-European vegetation and geomorphology of Yorke Peninsula, South Australia (after DWLBC 2005). EP = Eyre Peninsula; BALA = Balgowan assemblage; INPA = Innes National Park assemblage; TRHA = Troubridge Hill assemblage; Black = ephemeral salt lakes; Dark grey = Dryland Tea-tree – Drooping Sheoak low open woodland on calcrete; Light grey = Mallee on sand; White = other.

Study area

Yorke Peninsula experiences a Mediterranean climate with mild wet winters and hot dry summers (Neagle 2008). Southwestern Yorke Peninsula receives a mean annual precipitation of 478.3 mm (average of 48 years of data collected intermittently between 1893 and 2010 from Marion Bay, Innes National Park and Stenhouse Bay weather stations combined; Bureau of Meteorology 2011), whereas southeastern Yorke Peninsula receives a mean annual precipitation of 411.4 mm (average of 122 years of data collected between 1875 and 2001 from Edithburgh Post Office weather station; Bureau of Meteorology 2011).

Southern Yorke Peninsula has two distinct surface substrates derived from different sedimentary processes and the underlying Bridgewater Formation (Milnes and Ludbrook 1986). The two substrates support different vegetation associations (Figure 1; Department of Water, Land and Biodiversity Conservation [DWLBC] 2005). Mobile calcareous sands derived from coastal dunes dominate the western part of southern Yorke Peninsula where the Innes National Park assemblage (INPA) was found (DWLBC 2005). Prior to European colonization, this substrate supported Kingscote Mallee–Coastal White Mallee (*Eucalyptus rugosa–E. diversifolia*) associations with patches of vegetation dominated by White Mallee (*E. dumosa–E. phenax*) (Croft 2008). Remnants of this vegetation indicate a shrubby understorey that includes Dryland Tea-tree (*Melaleuca lanceolata*), Mallee Wreath Wattle (*Acacia triquetra*), Rock Wattle (*A. rupicola*) and Wedge-leaved Pomaderris (*Pomaderris obcordata*). By contrast, the surface geology of the eastern part of southern Yorke Peninsula, where the Troubridge Hill assemblage (TRHA) was found, is dominated by a discontinuous cover of shallow loamy calcareous soil overlying calcrete (DWLBC 2005). Before European colonization, this region supported Dryland Tea-tree–Drooping Sheoak (*M. lanceolata*–*Allocasuarina verticillata*) low open woodland (Croft 2008) around and within the numerous ephemeral salt lakes and associated gypsum deposits that occur in the area (DWLBC 2005). The understorey was probably open and grassy with sparse shrubs or understorey trees (Croft 2008). This vegetation association occurs on the majority of the west coast of Yorke Peninsula, including the area where the Balgowan assemblage (BALA) was found (Figure 1).

Yorke Peninsula was officially settled by European farmers in 1846 (Carmichael and Mudie 1973). It has been subjected to such extensive clearing and landscape modification, that Aitken (1973, p. 156) observed that “Few regions of South Australia have such a depleted fauna of native mammals as Yorke Peninsula”. He listed only eight non-volant native terrestrial mammal species: one monotreme *Tachyglossus aculeatus*, and seven marsupials *Sminthopsis crassicaudata*, *Lasiorhinus latifrons*, *Trichosurus vulpecula*, *Macropus eugenii*, *Macropus fuliginosus*, *Macropus robustus* and *Cercartetus concinnus*, collected from the Peninsula following European settlement, but did not specify localities. Of these *M. eugenii* have since been lost, though *L. latifrons and T. vulpecula* may still be present (Robinson *et al*. 2000a). Only three native non-volant terrestrial mammals (*T. aculeatus*, *M. fuliginosus* and *C. concinnus*) remain extant in Innes National Park (DEH 2003), although *M. eugenii* has recently been re-introduced (DEH 2004). The absence of *Rattus fuscipes* from the modern Yorke Peninsula fauna is probably due to the presence of introduced *Rattus rattus* (Brandle 2008), which can competitively exclude *R. fuscipes* (Cox *et al*. 2000).

Methods

AMS radiocarbon dating

Three complete long bones of *Perameles* each weighing approximately 1 g were selected from both the INPA and TRHA and submitted to the Waikato radiocarbon laboratory for AMS dating. Samples were processed using standard ultrafiltration AMS radiocarbon techniques (see Beaumont *et al*. 2010). Fossils from BALA were not radiocarbon dated because all specimens are highly weathered and considered unlikely to contain datable collagen. Ages were calibrated to the SHCal04 Southern Hemisphere calibration curve (McCormac *et al.* 2004) using OxCal v4.1.7 (Bronk Ramsey *et al.* 2010).

Collection and analysis

Fossils were collected from unstratified, calcareous sediments found in shallow coastal caves and a deflated sand dune. The INPA (Figure 1) was collected by C Kemper, P Rismiller, L Jansen and M Ayre in March 1988. The initial sample of the TRHA (Figure 1) was collected by T Worthy and A Camens in November 2008. A second sample was collected from this site by one of the authors (MCM) in April 2011. The BALA (Figure 1) was collected from a lag deposit on a deflated sand dune by M Fuller over a number of visits between 1986 and 1988. The BALA collection is held in the South Australian Museum (SAM) Palaeontology collection and the INPA and TRHA are held in the SAM Mammal collection.

Fossils from INPA and TRHA were initially handpicked from the cave floor. When the absence of stratigraphy became evident the top 10 cm of sediment from a small area of the floor was excavated and gently sieved through 1.5 mm mesh. Concentrated samples were then wet sieved and sorted to separate diagnostic bones which were picked out with forceps and stored in labeled containers. Fossils from BALA were handpicked from the dune surface. Diagnostic bones (whole and part skulls, maxillae, dentaries and/or teeth) were identified using published descriptions and comparative material held by the SAM. All specimens were identified to the lowest taxonomic level possible (usually species). The minimum number of individuals (MNI) was determined by counting the number of the most common diagnostic element of each species in each assemblage. To facilitate comparisons between samples, MNI was converted to relative abundance (Ri%), an expression of the MNI of a given species as a proportion of the total MNI for that collection. Richness (S) and Buzas-Gibson Evenness (E) indices were calculated to compare structural differences between each fossil assemblage. Prey mass was used to characterize accumulation agents. Mean adult body masses for all species were derived from van Dyck and Strahan (2008).

Table 1. AMS Radiocarbon ages of bones from Innes National Park assemblage (INPA) and Troubridge Hill assemblage (TRHA), Yorke Peninsula, South Australia

Sample	Waikato	Radiocarbon	Calibrated
INPAa	Wk-30728	181 ± 27	228–165
INPAb	Wk-30729	235 ± 27	222–146
INPAc	Wk-30730	223 ± 27	227–142
TRHAa	Wk-30731	797 ± 27	728–661
TRHAb	Wk-30732	915 ± 26	806–727
TRHAc	Wk-30733	994 ± 25	921–798

Results

AMS radiocarbon dating

AMS radiocarbon ages obtained from INPA and TRHA (Table 1) indicate that both assemblages were deposited within the last millennium. The INPA had a maximum age span of between 228 and 142 calBP, and appears to have accumulated very quickly. By contrast, TRHA had a maximum age span of between 921 and 661 calBP years. Because it accumulated more slowly, the TRHA may have experienced greater time averaging and may therefore have incorporated a greater number of rare species. However, as over half of the specimens recovered were attributable to a single species (Table 2), time averaging may have had minimal affect. The absence of the introduced house mouse, *Mus musculus*, from INPA and the occurrence of only a single specimen in TRHA are consistent with the radiocarbon ages.

Faunal Analysis

Thirty-one mammal species represented by a minimum of 1314 individuals were recovered from the three Holocene fossil assemblages examined (Table 2). Collections from both INPA and TRHA were composed predominately (>98%) of mammals weighing 200 g or less (Table 3). Mammals that weigh more than 200 g were rare and all represented by juveniles. In contrast, the collection from BALA was composed almost entirely of mammals that weighed more than 500 g (>98%; Table 3). The species compositions from the three assemblages also differed dramatically. Only two species (*Isoodon obesulus* and *Perameles bougainville*) were recorded from all three assemblages and only one additional species (*Macrotis lagotis*) occurred in both the BALA and TRHA. No other species occurred in both INPA and BALA. Many species occur in both the INPA and TRHA, but with the exception of *Notomys mitchellii*, these species are typically rare in either one or both

Table 2. The late Holocene non-volant mammal fauna of Yorke Peninsula, South Australia: minimum numbers of individuals (MNI) and relative abundances (Ri%) of species recorded from three sites, Balgowan assemblage (BALA), Innes National Park assemblage (INPA) and Troubridge Hill assemblage (TRHA); m = modern fauna (after Aitken 1973); p = present fauna (after Robinson *et al.* 2000a); - = not recorded; species mean adult mass (after van Dyck and Strahan, 2008). * = Body mass unknown, estimate only; † = introduced species.

	MNI			Ri%			European	Mean adult
Species	INPA	TRHA	BALA	INPA	TRHA	BALA	record	mass (g)
Dasyurus geoffroii	-	2	-	-	0.34	-	m	890
Dasyurus sp. indet.	-	2	-	-	0.34	-	-	-
Phascogale calura	1	3	-	0.15	0.51	-	-	51.5
Sminthopsis crassicaudata	3	9	-	0.45	1.52	-	m	15
Sminthopsis griseoventer	67	-	-	10.1	-	-	-	17.5
Sminthopsis sp. cf. *S. dolichura*	2	10	-	0.3	1.68	-	-	13.6
Sminthopsis sp. indet.	10	1	-	1.51	0.17	-	-	-
Isoodon obesulus	11	3	3	1.66	0.51	5.08	-	755
Perameles bougainville	3	7	1	0.45	1.18	1.69	-	215
Macrotis lagotis	-	2	1	-	0.34	1.69	-	1650
Trichosurus vulpecula	-	-	2	-	-	3.39	m	2850
Bettongia lesueur	-	-	1	-	-	1.69	-	1280
Bettongia penicillata	-	-	14	-	-	23.7	-	1300
Potorous platyops	2	-	-	0.3	-	-	-	1000*
Lagorchestes leporides	-	-	6	-	-	10.2	-	2000*
Macropus eugenii	-	-	6	-	-	10.2	m	6500
Macropus sp. cf. *M. fuliginosus*	-	-	15	-	-	25.4	p	>28000
Lagostrophus fasciatus	-	-	6	-	-	10.2	-	1600
Cercartetus concinnus	11	-	-	1.66	-	-	p	13
Pseudocheirus sp. cf. *P. peregrinus*	-	1	-	-	0.17	-	-	395
Leporillus apicalis	1	18	-	0.15	3.03	-	-	<150
Notomys mitchellii	195	89	-	29.5	15	-	-	52
Pseudomys australis	8	315	-	1.21	53	-	-	40
Pseudomys gouldii	17	30	-	2.57	5.05	-	-	45
Pseudomys occidentalis	105	3	-	15.9	0.51	-	-	34
Pseudomys shortridgei	49	1	-	7.41	0.17	-	-	70
Pseudomys or *Notomys* sp. indet.	25	29	-	3.78	4.88	-	-	-
Rattus fuscipes	150	68	-	22.7	11.5	-	-	92.5
Rattus tunneyi	1	-	-	0.15	-	-	-	66
Canis lupus dingo	-	-	1	-	-	1.69	-	14000
Mus musculus†	-	1	-	-	0.17	-	p	10
Oryctolagus cuniculus†	-	-	1	-	-	1.69	p	1580
Bos taurus†	-	-	1	-	-	1.69	-	>500000
Vulpes vulpes†	-	-	1	-	-	1.69	p	6150
Richness (S)	16	16	14	-	-	-	-	-
Buzas-Gibson Evenness (E)	0.41	0.27	0.61	-	-	-	-	-
Totals	661	594	59	100	100	100	-	-

of the assemblages. INPA is dominated by *Sminthopsis griseoventer, N. mitchellii, Pseudomys occidentalis* and *R. fuscipes*, TRHA is dominated by *Pseudomys australis* and to a lesser extent *N. mitchellii* and *R. fuscipes*, and BALA is dominated by macropodids (kangaroos and kin). This is reflected in the richness and evenness of the assemblages (Table 2). BALA was slightly less rich than the other two assemblages but richness did not differ greatly. However, Buzas-Gibson Evenness indicated that BALA had the most evenly distributed species abundance. TRHA had the least evenly distributed species whilst species from the INPA were moderately evenly distributed.

Table 3: Mean adult body mass distributions of late Holocene non-volant mammal species recorded from, Balgowan assemblage (BALA), Innes National Park assemblage (INPA) and Troubridge Hill assemblage (TRHA), on Yorke Peninsula, South Australia (after van Dyck and Strahan, 2008).

Mass (g)	INPA (%)	TRHA (%)	BALA (%)
0–100	97.39	94.16	0
101–200	0.65	4.21	1.69
201–300	0	0	0
301–400	0	0.17	0
401–500	0	0	0
>501	1.96	1.46	98.31

Discussion

Systematics

Of the 31 species identified in this study, three were assigned to species with caution. Specimens identified as *Sminthopsis* sp. cf. *S. dolichura* (Table 2) were distinguished from *S. griseoventer* and *S. aitkeni* by the following characters: M^3 metacristid shorter or subequal to, rather than longer than its crown length; dP^3 has three major cusps rather than two; C_l crown taller rather than subequal or shorter than that of P_1; very small entoconids on M_2 and M_3 (Kitchener *et al.* 1984). Differentiating between fragmentary specimens of *S. dolichura* and *S. murina* is much more difficult.

Maxillae appear morphologically indistinguishable and lower molars of both species have very small or absent entoconids.in addition, fossil specimens rarely retain all of their teeth, so key diagnostic features are not always preserved. As *S. griseoventer* occurs sympatrically with *S. dolichura* on Eyre Peninsula today (Kemper *et al*. 2011) and *S. murina* has never been recorded west of the Flinders Lofty Block, these specimens probably represent *S. dolichura* rather than *S. murina*, but cannot be diagnosed with absolute confidence.

Yorke Peninsula lies well outside the known distribution of *M. giganteus*, but fragmentary remains of *M. fuliginosus* appear morphologically indistinguishable from *M. giganteus*. Therefore, specimens from Yorke Peninsula are referred to *Macropus* sp. cf. *M. fuliginosus* reflecting the species that presently occurs in the area. For similar reasons the specific identity of the *Pseudocheirus* specimen is also unclear. Fragmentary crania of *Pseudocheirus occidentalis* and *Pseudocheirus peregrinus* appear to be indistinguishable (Baverstock *et al*. 1990). On the basis of then-unpublished research, Ride (1970) synonymized several named forms of *Pseudocheirus*, including *Pseudocheirus occidentalis*, with *P. peregrinus*. Although early molecular systematic data indicated considerable complexity within Ride's concept of *P. peregrinus*, McKay (1988) maintained the synonymy. However, *Pseudocheirus occidentalis* and *P. peregrinus* are now considered separate species (Burbidge and de Tores 1998; de Tores 2008). As the study area is closer to the known range of *P. peregrinus* than that of *Pseudocheirus occidentalis*, the taxon is referred to here as *Pseudocheirus* sp. cf. *peregrinus*.

If the tentatively made species identifications (Table 2) are correct, then, with the exceptions of *L. latifrons, Lagorchestes leporides* and *P. australis*, the native non-volant mammals recorded from Yorke Peninsula all consist of species that are either currently considered to be conspecific with populations recorded from southwestern Australia, or have been considered so in the past. The Australian arid zone cuts the late Holocene southern coast where the limestone karst Nullarbor Plain reaches the coast at the Head of the Great Australian Bight in far western South Australia. This has long been identified as a potential barrier between eastern and western biotas (e.g. Main *et al.* 1958; Parsons 1969). The extinction of many and in some cases all of the relevant populations of many mammal species since European colonization has rendered investigation of these east–west relationships much more difficult.

Accumulation agents

The INPA and TRHA were both found in shallow caves in coastal cliffs and were predominately composed of small mammals that weighed <200 g (Table 3), characteristics that are indicative of tytonid owl accumulations (Andrews 1990; Baird 1991; Higgins 1999). However, the BALA was collected from a surface lag deposit on a deflated sand dune. Its fauna is composed entirely of species that weighed >200 g (Table 3), the remains of which were associated with charcoal indicative of an Aboriginal midden (Coutts 1966). As different accumulation agents necessarily impose different biases on the assemblages they produce, quantitative palaeoecological comparison between owl assemblages (INPA; TRHA) and Aboriginal midden assemblages (BALA) cannot be made. However, contrasting assemblages deposited by different accumulation agents may provide a more complete appreciation of Yorke Peninsula’s Holocene mammal fauna. Differing accumulation agents may explain compositional differences between BALA and the other two assemblages, but not differences in the composition of INPA and TRHA. Avenant (2005) showed that frequencies of barn owl prey in South Africa closely matched the frequencies of prey available in the surrounding small animal community. In addition, studies have shown that Australian barn owls, which are typically nomadic and follow rodent irruptions, can have considerable dietary flexibility and are capable of consuming a diet consisting primarily of marsupials (Heywood and Pavey 2002) or even reptiles (McDowell and Medlin 2009). Therefore, the differences of species presence and frequency observed between INPA and TRHA are likely to represent differences in the proximal living communities at the time(s) of predation.

Assemblage composition and diversity

Our analysis of the INPA reveals that several now locally extinct mammal species persisted on southern Yorke Peninsula until European settlement (Table 2). It is also possible that species recorded from TRHA persisted until European settlement. These include *Phascogale calura, S. griseoventer, Potorous platyops, Leporillus apicalis, Pseudocheirus* sp. cf. *P. peregrinus* and *Lagostrophus fasciatus*, which had not previously been reported from the study area. The last two represent new records for Yorke Peninsula.

Whilst the INPA and TRHA share many species in common (Table 2), *S. griseoventer, I. obesulus, C. concinnus, P. platyops, N. mitchellii, Pseudomys occidentalis, R. fuscipes* and *Rattus tunneyi* are either unique to, or more abundant in, the INPA. In contrast, *Dasyurus geoffroii, M. lagotis, Pseudocheirus* sp. cf. *P. peregrinus, L. apicalis* and *P. australis* are either unique to, or much more abundant in the TRHA.

The species that characterize the INPA either require higher precipitation, sandy substrates or prefer mallee with heath understorey vegetation. Brandle (2010) found that *S. griseoventer* occurred in a range of mallee communities with a shrubby understorey of *Melaleuca* species on a variety of soils with light calcareous strew cover. This species has also been detected on sandy substrates (Crowther *et al*. 1999) and in heath woodland on coastal plains (Dickman 1988). *Isoodon obesulus* is known to occupy a number of vegetation communities. However, they generally include a combination of sandy soil and dense heath (Paull 2008). The nest sites of *C. concinnus* have been reported to be associated with sandy substrates (Morrant and Petit 2011) and *E. diversifolia*, *E. rugosa*, and *Melaleuca* spp. are considered important sources of dietary nectar and pollen (Pestell 2005; Pestell and Petit 2007). The occurrence of *C. concinnus* in the fossil record on southern Yorke Peninsula suggests that, unlike southern Eyre Peninsula (McDowell and Medlin 2010), mallee communities were well-established components of the pre-European vegetation rather than the result of European disturbance. *Notomys mitchellii* is also typically associated with sandy habitats (Watts and Aslin 1981; Brandle 2010) and mallee areas (Robinson *et al*. 2000b). *Rattus fuscipes*, though best considered an ecological generalist, is frequently found in coastal heathlands or forests with a heath understorey, but has also been detected on limestone and sand islands that support a chenopod shrubland (Robinson *et al*. 2000b).

Pseudomys occidentalis is a poorly understood species that was widely distributed across southern Australia prior to European colonization (Whisson 2008), but never collected alive in South Australia. Some researchers have suggested that the species was in decline before the arrival of Europeans (Watts and Aslin 1981; Lee 1995), but its abundant occurrence in an assemblage radiometrically dated to the approximate time of European colonization of Australia shows otherwise. *Pseudomys occidentalis* appears to be highly sensitive to fire and apparently prefers patches of extremely dense, long unburnt (between 30 and 50 yrs) vegetation on sandy clay loam or sandy loam (Whisson 2008). It is typically assumed that prior to European colonization fires were managed by Aborigines. The abundance of *Pseudomys occidentalis* in the INPA suggests that the area was infrequently burnt or burnt in patches. Near absence of the species from the TRHA probably reflects its preference for dense vegetation rather than more frequent fire.

Pseudomys australis is by far the most abundant species in the TRHA, in which it contributes >50% of the relative abundance (Table 2). The fossil distribution of this species indicates that it was much more widely distributed in the past but is now restricted to gibber with cracking clay areas in the Lake Eyre Basin (Robinson *et al*. 2000b; Brandle *et al*. 1999). These environmental conditions were probably replicated on southern Yorke Peninsula by areas of exposed calcrete associated with ephemeral lakes that would provide the gypsum-rich cracking clays that the species uses for shelter and nesting. However, the coastal form attributed to this species in the Yorke Peninsula assemblages is somewhat larger than the extant desert form and may represent either an example of Bergmann’s rule or potentially a hitherto unrecognized distinct species.

Other species that distinguish the fauna of TRHA from INPA include *D. geoffroii, M. lagotis, Pseudocheirus* sp. cf. *P. peregrinus and L. apicalis*. With the exception of *Pseudocheirus* sp. these species could once be found throughout the more arid areas of Australia but unlike *D. geoffroii* and *M. lagotis*, *L. apicalis* is not thought to have occurred on Yorke Peninsula post European settlement (van Dyck and Strahan 2008). *Leporillus apicalis* are thought to have built their nests in hollow tree limbs, caves and rock overhangs (Baynes 1987; Copley 1999 and references therein). *Leporillus apicalis* occurred primarily on calcareous but occasionally gypseous and/or saline soils that supported perennial shrublands composed primarily of chenopods (e.g. *Atriplex* spp. and *Maireana* spp.) nitre-bush (*Nitraria billardierei*) and pigfaces (e.g. *Carpobrotus* spp.) (Medlin 1993; Copley 1999). These succulent plants are thought to have made up a large proportion of the diet of both *Leporillus* species (Copley 1999). Therefore, *L. apicalis* may have been associated with the ephemeral salt lakes that occur in the study area (Croft 2008). However, Douglas (1980) identified sandalwood and quandong (both *Santalum* spp.) seeds as an important dietary component in more arid parts of this rodent's range.

Viewed together, the three assemblages investigated in this study yielded 27 species of native mammal, suggesting that the diversity of Yorke Peninsula's pre-European fauna was comparable with the mammalian diversity found in other studies (e.g. Watts and Ling 1985; Baynes 1987; Copley *et al.* 1989; McDowell and Medlin 2010). However, if considered individually, the richness of mammals yielded by each individual assemblage is considerably lower (Table 2). Whilst these assemblages show similar richness, their evenness varies considerably. The evenness values obtained from the INPA and BALA indicate that a larger number of species shared greater abundance. The very low evenness of TRHA is congruent with its extremely high abundance of *P. australis*. The very high relative abundance of *P. australis* may result from its propensity to irrupt during resource pulses following high rainfall, a phenomenon that barn owls are quick to exploit (Pavey *et al*. 2008; McDowell and Medlin 2009). However, it is unlikely that the TRHA roost was used only during rodent irruptions and even though irruptions may periodically elevate the relative abundance of *P. australis,* it cannot explain why the species dominates the

TRHA but is almost absent from the INPA. Pavey *et al*. (2008) demonstrated that barn owls are capable of selective predation and have a preference for larger rodents. However, assuming all owls are equally selective, the differences in the evenness of the TRHA and INPA cannot be explained by this phenomenon.

Factors that could influence the mammal richness, evenness and composition in a fossil assemblage include the accumulation agent (each with their inherent sampling biases), the prevailing climatic conditions experienced at the time of deposition and differences in local ecological constraints such as substrate, vegetation and fire frequency. However, it is most likely that differences in evenness reflect the levels of homogeneity of the ecosystems surrounding the assemblage locations.

Climatic conditions

Climate change is a driving force for faunal change and evolution (Hadly 1996; Barnosky and Bell 2003; Barnosky 2008) and may affect the diversity and distribution of mammals on a century and perhaps even decadal scale. Dodson (2001) found little change in the terrestrial vegetation of Australia's Mediterranean-type climate regions during the Holocene, implying that conditions have been relatively stable for much of the epoch. Numerous climate proxies indicate that 900 years ago, when the TRHA began accumulating, the Northern Hemisphere was experiencing the Medieval Warm Period, during which surface temperatures were equal to or greater than present (e.g. Tyson and Lindesay 1992; Nunn 2007; Mann *et al.* 2008; Jones *et al.* 2009). However, 200 years ago when the INPA was accumulating, the Northern Hemisphere was experiencing the tail end of the Little Ice Age, during which surface temperatures were cooler than present (Tyson and Lindesay 1992; Nunn 2007; Mann *et al.* 2008; Jones *et al.* 2009). Mann and Jones (2003) argued that even though fewer climate proxy records are available, surface temperatures in the Southern Hemisphere expressed a similar trend to the better-studied Northern Hemisphere record. While these periods correspond with the depositional times of TRHA and INPA respectively, the warmer and wetter period (Cobb *et al*. 2003) correlates with the more arid-adapted fauna of TRHA, suggesting little or no relationship between these global climate trends and local faunal composition.

The compositional differences between the INPA and TRHA correlate well with Yorke Peninsula’s historical rainfall distribution. The mean annual rainfall of western Yorke Peninsula, where the wetter-adapted fauna occurred, is 14% greater than that of eastern Yorke Peninsula, where the drier-adapted fauna occurs and may have influenced local ecological constraints enough to explain local differences in faunal composition.

Local ecological constraints

Small mammals typically have specific environmental requirements that dictate their distributions (e.g. Hadly 1999). Many require a particular precipitation level and vegetation communityfor feeding, nesting or to provide protection from predation. Others, particularly burrowing species, are restricted to specific substrates (e.g. Robinson *et al*. 2000b). The clear species compositional differences between the INPA and TRHA might best be explained by the distinctly different substrates and associated vegetation that occurred on southeastern and southwestern Yorke Peninsula (Figure 1). As these vegetation communities represent pre-European conditions (Croft 2008), relationships between fauna, flora and substrate can be inferred with confidence. TRHA and BALA share the same substrate and vegetation association (Dryland Tea-tree–Drooping Sheoak low open woodland on calcrete, see

Figure 1). However, marked differences in faunal composition between the two assemblages add further support to the conclusion that they are the product of different accumulation agents.

Biogeography

Yorke Peninsula's late Holocene mammal fauna can be separated into four groups:1) taxa that retain naturally occurring populations in both southeastern and southwestern Australia; 2) taxa that retain naturally occurring populations in both southeastern and southwestern Australia but whose taxonomic status has been unclear; 3) taxa that are locally extinct in southeastern Australia but still have naturally occurring populations in southwestern Australia; and 4) taxa that are extinct in both southeastern and southwestern Australia. Distribution maps in van Dyck and Strahan (2008) are utilized in the following discussion.

Sminthopsis dolichura and *M. fuliginosus* are examples of members of the Yorke Peninsula fauna that retain extant mainland populations both southwest and southeast of the Nullarbor. *Tachyglossus aculeatus, S. crassicaudata, S. griseoventer, I. obesulus*, *T. vulpecula*, *C. concinnus*, *N. mitchellii*, *P. shortridgei* and *R. fuscipes* also share this distribution pattern. Due to conservation concerns the distribution of *P. shortridgei* has been well studied. Cooper *et al.* (2003) found little genetic difference between southwestern and southeastern populations, but Salinas *et al.* (2009) found that Victorian and southwestern Australian specimens showed differentiation comparable to different species. They inferred that the two populations were isolated about 1.4 million years ago by aridity on the Nullarbor Plain. Although *P. shortridgei* was not recorded from surfaces of southern Nullarbor caves east of the western end of the Great Australian Bight by Baynes (1987), its remains are present in mid Holocene levels of Allen's Cave and Warbla Cave in the far west of South Australia (Baynes 1994, pers. obs. Kemper *et al.* 2010). During glacials continuous east-west populations may have existed in coastal dunes across what is now the Bight (Cooper *et al.* 2003). Little is known of the South Australian distribution of *P. shortridgei* between the mid-west and southeast (Kemper *et al.* 2010). It is possible that the major genetic discontinuity occurred across the Murray River valley and estuary where suitable heath habitats probably do not exist, rather than across the Nullarbor, although major genetic discontinuities may have occurred in both areas. Neaves *et al.* (2009) have demonstrated that such genetic discontinuities are unexpectedly common even in large vagile Australian mammals such as kangaroos. Remains of *P. shortridgei* are plentiful in South Australian assemblages, such as those on Yorke Peninsula, so this question should be resolvable using ancient DNA techniques. It would also be interesting to explore the affinities of the Kangaroo Island population, particularly if it is still extant (Kemper *et al.* 2010).

The genus *Pseudocheirus* also retains southwestern and southeastern populations that were once considered conspecific but have since been recognized as separate species. *Pseudocheirus* remains were recorded in surface material from three caves along the southern edge of the western Nullarbor, and ascribed to *P. peregrinus* (Baynes 1987). *Pseudocheirus* has also been recorded from late Holocene strata in Allen's Cave in the far west of South Australia (Baynes 1994), and from a Holocene site on southern Eyre Peninsula (McDowell and Medlin 2010; Table 4).

Table 4. (opposite) Native non-volant mammal faunas of Yorke and Eyre Peninsulas, South Australia. Eyre Peninsula is divided into a southwestern zone (south and west of the 400 mm mean annual rainfall isohyet, Schwerdtfeger 1985), comparable in area and rainfall range to Yorke Peninsula, and a northern and eastern zone of lower rainfall. Late Holocene and historic Eyre Peninsula mammal records from Watts and Ling (1985) and Baynes (1987) with modifications, McNamara (1997), McDowell and Medlin (2010) (southwestern zone only) and Kemper *et al*. (2011). Vernacular names from van Dyck and Strahan (2008). f = fossil record; m = modern record; ? = less certain record; - = not recorded; † = introduced species.

Species	Yorke Peninsula	SW Eyre Peninsula	NE Eyre Peninsula
Tachyglossus aculeatus (Short-beaked Echidna)	m	m	m
Antechinomys laniger (Kultarr)	-	-	m, f
Dasycercus sp. indet. (Brush- or Crest-tailed Mulgara)	-	f	-
Dasyurus geoffroii (Western Quoll)	f	f	?
Ningaui yvonneae (Southern Ningaui)	-	-	m, f
Parantechinus apicalis (Dibbler)	-	f	-
Phascogale calura (Red-tailed Phascogale)	f	-	f
Phascogale tapoatafa (Brush-tailed Phascogale)	-	?	-
Sminthopsis crassicaudata (Fat-tailed Dunnart)	f	-	f
Sminthopsis dolichura (Little Long-tailed Dunnart)	m, f	f	m
Sminthopsis griseoventer (Grey-bellied Dunnart)	f	f	m
Sminthopsis macroura (Stripe-faced Dunnart)	-	-	m
Sminthopsis psammophila (Sandhill Dunnart)	-	-	m, f
Isoodon obesulus (Southern Brown Bandicoot)	f	f	-
Perameles bougainville (Western Barred Bandicoot)	f	f	f
Macrotis lagotis (Greater Bilby)	f	f	?
Lasiorhinus latifrons (Southern Hairy-nosed Wombat)	m	m, f	m
Trichosurus vulpecula (Common Brushtail Possum)	m, f	f	m
Bettongia lesueur (Burrowing Bettong)	f	f	f
Bettongia penicillata (Brush-tailed Bettong)	f	f	?, f
Potorous platyops (Broad-faced Potoroo)	f	f	f
Lagorchestes leporides (Eastern Hare-wallaby)	f	-	-
Macropus eugenii (Tammar Wallaby)	f	f	?
Macropus fuliginosus (Western Grey Kangaroo)	m, f	m, f	m
Macropus robustus (Euro)	m, f	-	m
Macropus rufus (Red Kangaroo)	-	-	m
Petrogale xanthopus (Yellow-footed Rock-wallaby)	-	-	m
Lagostrophus fasciatus (Banded Hare-wallaby)	f	-	f
Cercartetus concinnus (Western Pygmy-possum)	m, f	f	?, f
Pseudocheirus sp. cf. *P. peregrinus* (Ringtail Possum)	f	f	-
Leporillus apicalis (Lesser Stick-nest Rat)	f	-	f
Notomys mitchellii (Mitchell’s Hopping-mouse)	f	f	m, f
Pseudomys australis (Plains Mouse)	f	f	f
Pseudomys bolami (Bolam’s Mouse)	-	f	f
Pseudomys gouldii (Gould’s Mouse)	f	f	f
Pseudomys occidentalis (Western Mouse)	f	f	f
Pseudomys shortridgei (Heath Mouse)	f	f	f
Rattus fuscipes (Bush Rat)	f	m, f	f
Rattus tunneyi (Pale Field-rat)	f	f	-
Canis lupus (Dingo)	f	f	m
Total species	30	28	33+

Dasyurus geoffroii, *P. calura*, *Bettongia penicillata* and *Pseudomys occidentalis* comprise a third species group whose naturally occurring mainland populations persist only in the southwest, having become extinct in southeastern Australia. *Macropus eugenii* shows a variation on this pattern, surviving on Kangaroo Island in South Australia.

The final group consists of species in which both southeastern and southwestern mainland populations are extinct (though some survive on islands or in northern Australia). These species include *P. bougainville*, *M. lagotis*, *Bettongia lesueur*, *P. platyops*, *L. fasciatus*, *L. apicalis*, *P. gouldii* (encompassing *P. fieldi*) and *R. tunneyi*. Of these, *L. fasciatus* has long been known from South Australian mid Holocene deposits (e.g., McNamara 1997) and was recently shown to have been extant and widespread, though subspecifically distinct, in South Australia when colonized by Europeans (Helgen and Flannery 2003).

The pre-European fauna of Yorke Peninsula is highly comparable in both species composition and diversity to that recorded from southwestern Eyre Peninsula (Table 4). Both regions are similar in area and climate (Schwerdtfeger 1985; DEH 2003) and following Holocene sea-level rise would have formed virtual islands for terrestrial fauna, isolated by the Southern Ocean to the south and aridity to the north. The 27 species recorded from southwestern Eyre Peninsula include two dasyurids not recorded from Yorke Peninsula: *Dasycercus* sp. indet., widespread in sandy habitats in the arid zone, and *Parantechinus apicalis,* at its most easterly known occurrence *Pseudomys bolami* is also recorded from Eyre Peninsula but not Yorke Peninsula. Mammals recorded from Yorke Peninsula but not southwestern Eyre Peninsula include *P. calura*, *L. leporides*, *L. fasciatus* and *L. apicalis*. This is the most westerly occurrence of *L. leporides* known; the other three species have been recorded from northern Eyre Peninsula (Table 4). An additional six species were recorded from northern Eyre Peninsula only, though all were once widespread in the arid zone (Table 4).

Conclusions

The faunal compositions of the three Holocene fossil assemblages we investigated are distinctly different. The differences between the BALA fauna and those of the more southerly assemblages are most likely due to differing accumulation agents. Evidence suggests that BALA was accumulated by humans, but that INPA and TRHA were accumulated by owls. Whilst assemblages accumulated by different accumulation agents may not be quantitatively comparable, they form an ensemble that provides a more complete representation of a region’s fauna than can be gained from any single site.

The segregation of small mammal species on southern Yorke Peninsula was probably driven by local ecological constraints. Species that show preferences for mallee, sandy substrates and dense vegetation occur predominately or exclusively in the INPA. In contrast, many of the species that occur predominately or exclusively in the TRHA show preferences for stony, loamy and cracking clay substrates and more open woodland with a shrubland and grassland understorey. The high degree of habitat fidelity to known ecological constraints or preferences shown by the Yorke Peninsula fossil faunas provides support for the assumption of uniformitarianism that palaeoecologists are typically forced to make. However, given the close proximity of the INPA and TRHA and their extensive composition differences, this study also demonstrates the risk of geographically over-extrapolating palaeoecological data, particularly in regions of heterogeneous habitat.

It is clear that before the arrival of Europeans the native non-volant mammal fauna of Yorke Peninsula was much more diverse than that of today. By establishing the age of the analyzed assemblages we demonstrate that climate change played little or no part in the extirpation or extinction of these mammals. Europeans are probably responsible through habitat destruction, introduction of exotic competitors, predators and/or hunting. However, more data are needed before we can determine the relative impacts of each mechanism.

This research highlights the potential Holocene fossil assemblages have for providing baseline data to natural resource managers, informing on the composition, richness, evenness and heterogeneity of pre-European faunas. In addition, studies of this type are valuable to conservation managers because they identify species that may be re-introduced to a site as part of ecosystem restoration programmes. Investigation of the biogeography of species identified in this study show strong faunal affinities between Yorke Peninsula and southwestern Eyre Peninsula. This suggests that prior to Holocene sea-level rise mammal populations were continuous between the peninsulas and across the intervening lower-lying area that is now Spencer Gulf.

AMS radiocarbon dating established that the INPA and TRHA were of late Holocene age and suffered little from the effects of time averaging. Whilst this research supports the frequently made assumption that surface and shallow unstratified deposits are typically of late Holocene origin, it is highly desirable that future research includes radiometric dating to avoid comparison of differently aged assemblages. The Bridgewater Formation undoubtedly perserves numerous yet-to-be-discovered Holocene fossil assemblages. As more are recovered, analyzed and dated, the ensuing composite fossil record may reveal the pressures that dictate the biogeography of Australia's pre-European fauna, and may provide insight into the processes that must be managed to preserve our remaining biodiversity.

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CHAPTER 6

Chronology, stratigraphy and palaeoenvironmental interpretation of a Late Pleistocene to mid-Holocene cave accumulation on Kangaroo Island, South Australia

Context

This chapter presents a detailed analysis of the sedimentology, stratigraphy, geochemistry and chronology of the Late Pleistocene–Holocene assemblage excavated from Kelly Hill Cave (5K1), Kangaroo Island.

Statement of authorship

I collected, prepared and analysed most of the material examined in this chapter (with additional support from those noted in the Acknowledgements). I supervised volunteers who assisted in excavation, preparation and analysis of sediments. I prepared the stratigraphic section, described the sediments, carried out grain-size analysis and analysed petrographic slides. I prepared grant applications to fund the majority of AMS radiocarbon dating acquired for the study. I prepared the original and final manuscript for publication.

Erick A. Bestland provided advice on sedimentary and petrographic analyses, commented on the draft manuscript and contributed to the discussion.

Fiona Bertuch conducted AMS radiocarbon dating and commented on the draft manuscript.

Linda K. Ayliffe calibrated and interpreted the U–Th dates, commented on the draft manuscript and contributed to the discussion.

John C. Hellstrom conducted the U–Th dating.

Geraldine E. Jacobsen coordinated AMS radiocarbon dating at Ansto, commented on the draft manuscript and contributed to the discussion.

Gavin J. Prideaux provided guidance and advice, commented on the draft manuscript and contributed to the discussion.

Chronology, stratigraphy and palaeoenvironmental interpretation of a Late Pleistocene to mid-Holocene cave accumulation on Kangaroo Island, South Australia

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Abstract

Chronological, sedimentological and geochemical analyses of a clastic infill from Kelly Hill Cave (5K1), Kangaroo Island, documents a palaeoenvironmental record that spans from the Late Pleistocene to the middle Holocene. We AMS radiocarbon dated bone collagen and U–Th dated speleothem to determine that fossiliferous sediments were deposited between >20 ka to 7 ka ago. Most of the 15 sedimentary layers are dominated by sand- and silt-sized quartz that is physically and geochemically comparable with surface soils in the Kelly Hill area. Late Pleistocene and Last Glacial Maximum strata are represented primarily by homogeneous, poorly sorted quartz-rich sediments that contain little organic matter, but also include a thin layer composed largely of silt-sized clay pellets that resemble sediments deflated from playa lakes. Microstructures observed in petrographic slides indicate that, with the exception of one layer, all sediments experienced little reworking once deposited in the cave. Some layers display pedogenic microstructures such as redeposited clays and opaline silica infilling that indicate post-deposition modification; i.e., cave floor soil development. Overlying Holocene-aged sediments also consist mainly of quartz but have much greater organic matter content. Some of these sediments have been strongly influenced by re-precipitated organic matter that appears to have been transported into the cave via vadose drip-water. The presence of dissolved organic matter in soil/vadose waters suggests high vegetation density and acidic soils which are congruent with the more equitable climatic conditions characteristic of the Holocene. The sediments described here provide a valuable palaeoenvironmental record that will facilitate future interpretation of associated vertebrate fossils.

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Research on palaeoclimate archives such as pollen sequences (Kershaw *et al*. 1991; Rule *et al*. 2012), wind strength, direction and dune-building (Bowler *et al*. 1976; Singh *et al*. 1981; Wasson 1984; Thom *et al*. 1994; Shulmeister *et al*. 2004; Fitzsimmons *et al*. 2007), fluvial deposits (Nanson *et al*. 1992), deep-sea sediments (Gingele *et al*. 2007; De Deckker *et al*. 2012), former lake levels (Galloway 1965;

Dodson 1974, 1975; Cohen *et al*. 2012) and speleothem growth (Ayliffe *et al*. 1998) have provided insight into Australia's climate history. Evidence suggests that southern Australia experienced a progressive drying trend during the Late Pleistocene that culminated in the Last Glacial Maximum (LGM), which persisted from approximately 22 to 17 ka ago (Barrows *et al*. 2002; Petherick *et al*. 2008). During this period southern Australia experienced increased evapotranspiration, wind strength, and up to 50% less precipitation than present (Bowler 1976; Bowler *et al*. 1976; Sprigg 1979; Jouzel *et al*. 1995; Dodson & Ono 1997; Hesse *et al*. 2004; De Deckker *et al*. 2012). Eustatic sea-levels were ~120 m lower than present (Chappell & Shackleton 1986; Yokoyama *et al*. 2001) and much of the continental-shelf was exposed (Yokoyama *et al*. 2001) connecting Australia's land-bridge islands to the mainland (Hope *et al*. 1977; Lampert 1981). Intense aridity and diminished vegetation cover caused the expansion of sand dunes which at their peak covered two-thirds of Australia and extended onto the western and southern margins of the exposed continental shelves (Bowler 1976; Sprigg 1979; Wopfner & Twidale 1988; McTainsh 1989; Nanson *et al*. 1992; Hesse and McTainsh 1999; Haberle 2005; Byrne *et al*. 2008). These conditions severely impacted biota, reducing biodiversity across southern Australia (Bradley 1999). After the LGM, rapid global warming caused ice sheets to melt which in turn caused a rapid rise in sea-level which reached present levels about 7 ka ago, re-isolating land-bridge islands from the mainland (Dodson 1998; Belperio & Flint 1999; Bradley 1999; Cutler *et al*. 2003). Rising sea-levels resulted in increasing precipitation and a reduction in strong wind regimes and temperature extremes, thus accommodating increasing biodiversity (e.g. White 1994; Forbes *et al*. 2007). In addition to the influences of climate change, continental islands are dramatically influenced by the waxing and waning of sea-level and therefore have the potential to preserve high resolution climate change histories.

Caves are highly efficient sediment traps that remain stable within a changing landscape and can accumulate excellent palaeoclimate proxies that are rarely duplicated in open-air sites (Collcutt 1979; Courty & Vallverdu 2001; White 2007). Cave sediments typically provide the accumulation and palaeoenvironmental context of palaeontological excavations. Therefore, sedimentary analyses are essential for palaeoecological interpretation and may provide insight into the impacts of past climate change, from which potential impacts of future climate change can be predicted (Forbes *et al*. 2007; Prideaux *et al*. 2007, 2010; Stewart & Cooper 2008; Macken *et al*. 2011). Cave sediments typically contain charcoal and bone which can be radiocarbon dated, and speleothems which can be U–Th dated. Combined, these two dating techniques provide a robust chronology, allowing correlation between cave sediments and climatic events (White 2007). However, cave sediments can be subject to complex erosional and depositional processes that may result in unconformities, lateral facies changes and stratigraphic reversals, complicating the reconstruction of their depositional history (Osborne 1984; Kos 2001). Detailed analysis of the macro- and micro-stratigraphic, physical and geochemical properties of cave sediments can help to overcome these difficulties and when combined with palaeontological findings, can contribute to the reconstruction of a sound palaeoenvironmental record of accumulation (Knapp *et al*. 2004; Forbes *et al*. 2007; Osborne & Jass 2008).

Australian late Quaternary cave sediment fills have been widely studied (e.g. Ayliffe & Veeh 1988; Osbourne 1991; Olley *et al*. 1997; Moriarty *et al*. 2000; Kiernan *et al*. 2001; Kos 2001; McDowell 2001; Pate *et al*. 2002, 2006; Forbes & Bestland 2007; Forbes *et al*. 2007; Prideaux *et al*. 2007; Ayliffe *et al*. 2008; Darrénougué *et al*. 2009; Prideaux *et al*. 2010; Quigley *et al*. 2010; Macken *et al*.

2011), but few encompass the LGM and Late Pleistocene–Holocene transition. Furthermore, the potential of cave accumulations on KI as archives of palaeoenvironmental information has been largely overlooked. Hope *et al*. (1977) and Lampert (1981) made cursory descriptions of the sediments excavated from Seton Rock Shelter (Fig. 1B), but primarily used the stratigraphy to provide a depositional context for faunal and cultural objects. The Kelly Hill Cave system (KHC; Fig. 1C) contains thick (at least 3.5 m) clastic fossiliferous accumulations that provide an opportunity to investigate how terrestrial fauna reacted to climate change and isolation. Most of the non-volant mammals preserved in the KHC fossil sequence are either extant of recently extinct, and include 10 species that have not previously been reported from KI (*Perameles gunnii, Acrobates pygmaeus, Cercartetus nanus, Potorous tridactylus, Onychogalea fraenata, Lagostrophus fasciatus, Hydromys chrysogaster, Notomys mitchellii, Pseudomys apodemoides, Pseudomys gouldii*) as well as two species of megafauna (‘*Procoptodon*’ *gilli* and ‘*Procoptodon*’ *browneorum*). In this study, we aim to (i) establish the chronology of an excavation in KHC using radiocarbon and U–Th dating, (ii) assess stratigraphic competence and depositional processes using macro- and micro-stratigraphic features, (iii) characterise the sediments excavated from the deposit to identify their potential sources by systematically analysing sediment colour, grain size, grain shape and geochemistry, and (iv) combine these data to deduce palaeoenvironmental change over time.

Geological setting and study area

Kangaroo Island, Australia’s third largest land-bridge island, is located off the coast of South Australia on a broad expanse of the continental-shelf (Fig. 1A). The island is approximately 145 km long east to west, 55 km at its widest north–south point and has an area of 4405 km^2 (Lampert 1981; Twidale & Bourne 2002). KI is currently separated from Yorke Peninsula to the north by Investigator Strait, a 50-km stretch of 30 metre deep water (Lampert 1981) and from Fleurieu Peninsula to the northeast by Backstairs Passage, a 14-km stretch up to 40 metres deep (Robinson & Armstrong 1999). Kangaroo Island sits on a foundation of Cambrian Kanmantoo Group metasediments which are capped by a lateritic plateau (Fig. 1; Belperio & Flint 1999; James & Clark 2002). Glacial erosion during the Late Carboniferous and early Permian carved deep valleys into this bedrock creating Backstairs Passage (Belperio & Flint 1999). Since then, KI has experienced a number of episodes of continental and marine sedimentation separated by periods of prolonged sub-aerial weathering and erosion (Belperio & Flint 1999). During the Pleistocene a widespread marine transgression deposited calcareous sandstones and limestones of the Bridgewater Formation (Fig. 1) that outcrop as high as 120 m above present sea-level at Kelly Hill and Mount Taylor (Sprigg 1979; Milnes *et al.* 1983; Hill 1984; Belperio & Flint 1999; Murray- Wallace 2002; Twidale & Bourne 2002; Shand *et al*. 2006).

The Bridgewater Formation covers much of the southern coast of KI (Belperio & Flint 1999) and predominantly supports low open mallee forest (Department for Environment, Heritage and Aboriginal Affairs 1999).

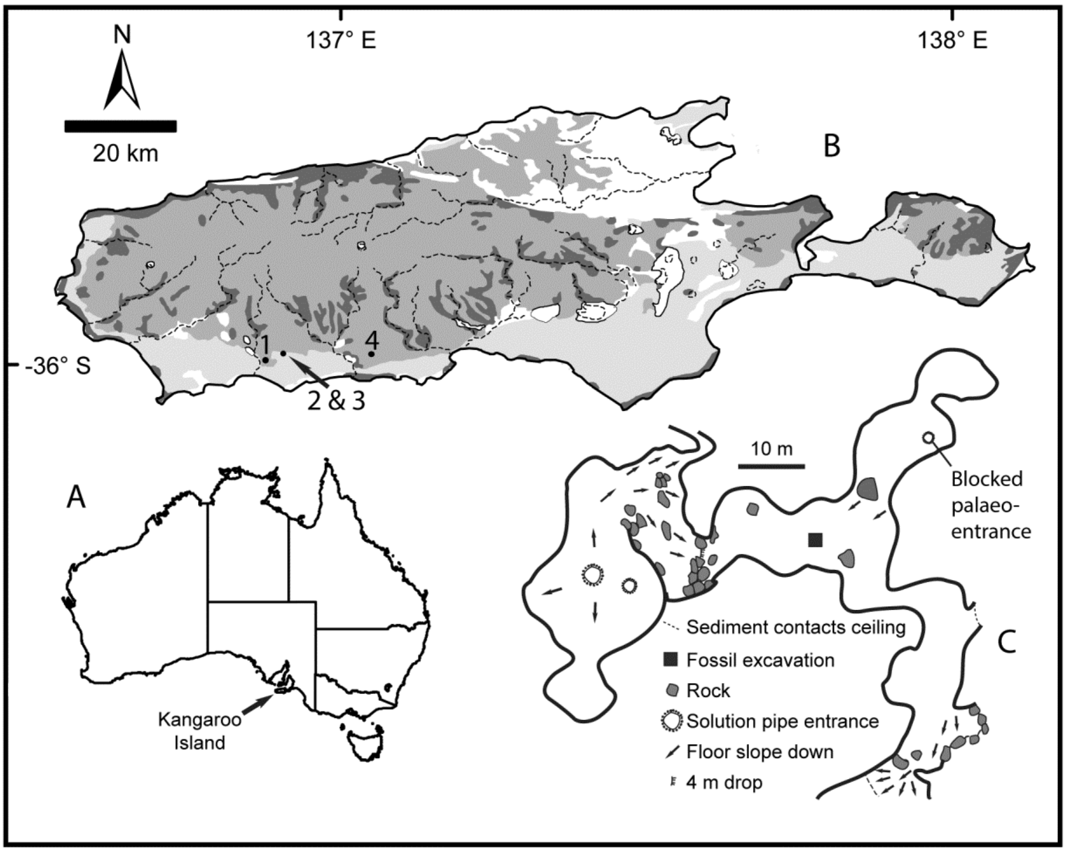


Fig. 1. A. Location of Kangaroo Island relative to the Australian mainland. B. Location of 1 = Grassdale surface samples. 2 = Kelly Hill Cave. 3 = Kelly Hill surface samples. 4 = Seton Rockshelter, Kangaroo Island. Dashed lines = drainage. Dark grey = Kanmantoo Group metasediments excised by drainage. Mid grey = Lateritic colluvium. Light grey = Bridgewater Formation. White = other sediment (after Raymond *et al*. 2012). C. Relevant map section of Kelly Hill Cave (after CEGSA map CEG 6001) showing the location of modern solution pipe entrances, fossil excavation and the blocked palaeo-entrance through which excavated sediments and bones entered the cave.

Genesis of the Kelly Hill Cave system

Limestone cave development is often controlled by joints and fissures in hard rocks through which meteoric water infiltrates, interacts with groundwater and cause limestone dissolution (Sprigg 1952; Jennings 1985). However, the KHC system, which consists of a series of cave entrances connected by extensive passages covering at least 36 000 m^2 (Lewis 1976), appears to have formed by a different process (Mooney 1983; Hill 1984; White 1994). Deposition of Pleistocene dune systems on KI blocked the creeks and rivers that drained the plateau causing the development of shallow lakes or swamps. This standing water slowly infiltrated the then poorly consolidated dune sediments at several points along the base of the dune resulting in the dissolution of large lateral cavities that have matured into structurally stable chambers (Mooney 1983; Hill 1984; Twidale & Bourne 2002).

Methods

Site selection and excavation

The excavation site was selected based on the presence of fossil bones on and in surface sediments, likelihood of stratigraphic integrity, likelihood of minimal disturbance, depth of sediment (determined using a 1.5-m steel probe) and presence of speleothem growth above the excavation site (suggesting potential speleothem deposition in the sediment). A 2 x 2 m^2 grid was established to delineate the excavation and was subdivided into four equal-sized quadrats. Most of the overlying anthropically disturbed sediment was removed, but a small amount still interpenetrated the *in situ* sediment when excavation began. To assess stratigraphy, two quadrats were initially excavated in 5-cm spits to a depth of 95 cm. Subsequent excavation was confined to the exposed sedimentary layers, but where a stratum was thicker than 5 cm, it was excavated in 5 cm spits to minimise time averaging. A representative bulk sample of each stratum was collected to determine its physical properties.

Radiocarbon dating

Complete, un-calcified postcranial bones and one tooth sample were selected for AMS radiocarbon dating (Table 1). At the Australian Nuclear Science and Technology Organisation (ANSTO) collagen was extracted from the bones and tooth dentine using a modified Longin technique with purification of the collagen using ultrafiltration (e.g. Brown *et al*. 1988; Higham *et al*. 2006). Rafter Radiocarbon Laboratory used a modified Longin method with filtration and Beta Analytic used a modified Longin method where bones were decalcified and the residue treated with acid/alkali/acid pretreatment method. Degraded collagen is susceptible to contamination from organic materials, particularly humic acids, which can then lead to inaccurate radiocarbon dates (Stafford *et al*. 1987; van Klinken & Hedges 1995), thus it is essential that both prior to and during processing, the bone and extracted collagen are tested to assess the degree of preservation and suitability for dating (Higham *et al*. 2006). Several methods for testing the degradation of the bone and/or extracted gelatin have been reported (DeNiro & Weiner 1988; van Klinken 1999). At ANSTO, the selection of suitable bones was based on nitrogen content (N%) of the bone, as this is a proxy for collagen content (DeNiro & Weiner 1988; van Klinken 1999). The quality of the extracted collagen was then determined using C:N ratio and collagen yield.

Table 1. Summary of radiocarbon and U–Th age estimates for the Kelly Hill Cave excavation derived using the OxCal 4.1 programme (Bronk Ramsay 2009). Age determinations for each method are presented in Tables S1 and S2 respectively. U–Th dating was applied to speleothem rafts and associated stalagmites that draped over the layer and spit indicated. Radiocarbon dating was applied to bone from the indicated layer and spit. ^{T} = tip and ^{B} = base of stalagmite; OZ = ANSTO lab code, NZA = Rafter Radiocarbon lab code, Beta = Beta Analytic lab code, UMD = University of Melbourne lab code, D = disturbed sediment.

Lab code	Unit	Layer	Depth	Calibrated radiocarbon age	U–Th
NZA 33928	D	1(S1)	3	7.89+0.08/–0.10	
OZN779	D	3(S1)	7	9.7+0.3/–0.1	
NZA 33933	1a	5(S1)	18	6.8+0.1/–0.1	
OZN781	1a	5(S1)	22	7.49+0.08/–0.06	
UMD120309-215	1a	5(S3)	30		6.9±0.4
OZN784	1a	6(S1)	34	7.37+0.08/–0.9	
UMD120309-217	1a	6(Surface)	43		7.4±0.3
OZN786	1b	7x(S1)	45	7.62+0.07/–0.09	
OZN787	1b	7y(S1)	45	7.60+0.08/–0.10	
OZN788	1b	8(S1)	55	7.9+0.1/–0.1	
UMD120309-225	1b	8(Surface)^{T}	53		7.3±0.5
UMD120309-226	1b	8(Surface)^{B}	53		9±1
NZA 33932	1b	8(S2)	59	8.8+0.2/–0.1	
UMD120309-242	1c	9(Surface)^{T}	63		10.8±0.5
UMD120309-302	1c	9(Surface)^{B}	63		9.7±0.4
OZO528	1c	9(S1)	64	10.0+0.2/–0.2	
OZO531	2	10(S1)	79	16.7+0.2/–0.3	
NZA 33977	2	10(S2)	80	9.4+0.1/–0.2	
Beta-320117	2	10(S2)	84	23.5+0.3/–0.5	
OZO532	2	10(S3)	88	17.4+0.4/–0.3	
UMD120309-311	3	11(Surface)	90		10.25±0.07
OZN793	3	11(S3)	102	19.4+0.3/–0.4	
UMD120309-312	3	11(S5)	103		19±1

Only collagen that passed the criteria of C:N ratio within the range 2.8–3.6 (DeNiro 1985; Ambrose 1990; van Klinken 1999) and with collagen yield >1% (van Klinken 1999) were then processed to graphite for AMS measurement on a HVE 2MV Tandetron; $\delta^{13}C$ and C:N ratio were determined using an elemental analyser isotope ratio mass spectrometer (EA-IRMS)(vario Micro cube EA, Elementar Germany and IsoPrime IRMS, GV Instruments, UK) (Fink *et al*. 2004). Rafter Radiocarbon and Beta Analytic used $\delta^{13}C$ ratios to assess collagen quality. Radiocarbon ages <11.0 cal. ka BP were calibrated using the SHCal04 calibration curve (McCormac *et al*. 2004). Radiocarbon ages >11.0 cal. ka BP were calibrated using the IntCal09 calibration curve (Reimer *et al*. 2009).

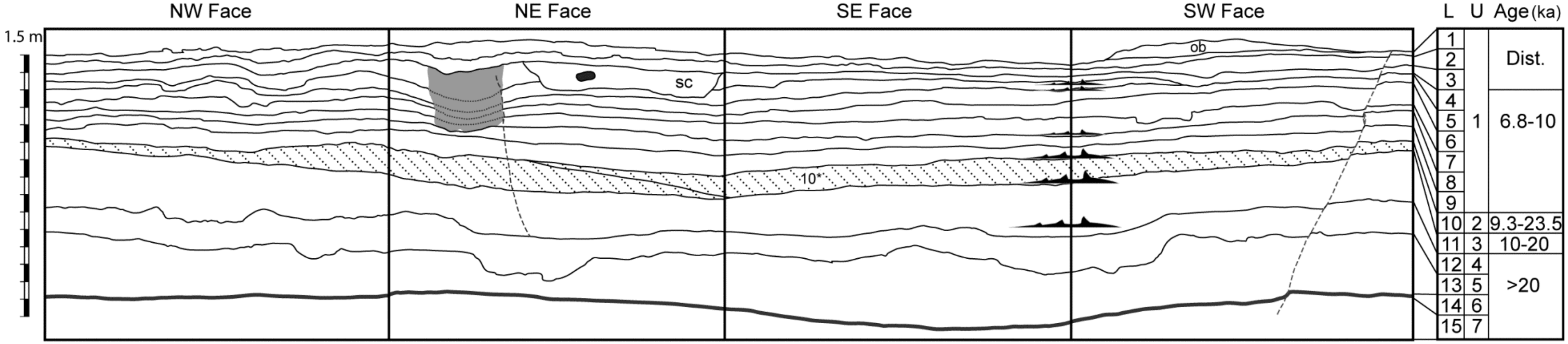
Uranium series dating

In situ speleothem rafts and associated stalagmites from layers 5, 6, 8, 9 and layer 11 (Fig. 2) of the KHC excavation were uranium series dated by multi-collector inductively-coupled plasma mass spectrometry according to the analytical protocols described by Hellstrom (2003). In addition, U and Th isotope measurements made on a recent stalagmite from a neighbouring chamber of KHC, analysed by Thermal Ionization Mass Spectrometry (following procedures outlined in Ayliffe *et al*. 1998), were used to assess the initial $^{230}Th/^{232}Th$ of detrital contamination in the cave system. This $[^{230}Th/^{232}Th]_{initial}$ estimate was then applied to the U and Th results from the speleothem found in the KHC excavation to correct for contributions from detrital ^{230}Th using equation 1 in Hellstrom (2006).

Sedimentary analyses

Sediment colour, grain shape and grain size were determined for each sedimentary layer identified in the excavation and six surface samples. The colour of sediments from each layer was determined from air-dried sediment using a Munsell Soil Colour Chart under natural light. Average grain roundness and sphericity were determined by observing a representative subsample of sediment from each layer under an Olympus SZX12 dissecting microscope at 50X magnification and compared with the Powers Roundness Scale (Powers 1953). Grain size was measured using Endecott sieves and a Malvern Mastersizer 2000 Laser Particle Sizer. 100 g of sediment from each layer was oven dried overnight at 100°C. Dried sediment was sieved into >2000 µm, 1000–2000 µm and <1000 µm sized fractions using Endecott sieves. Each fraction was weighed separately to determine the relative contribution it made to the sediment. The Mastersizer, which determines grain size distributions based on the obscuration of light by grains suspended in solution, was then used to measure particles from the <1000 µm fraction in accordance with manufacturer's instructions. Five grain-size distribution measurements were made for each sample from which averages were calculated. Grain size statistics for the <1000 mm fraction were calculated using Gradistat v8.0 (Blott & Pye 2001). Petrographic slides were prepared from articulated sediment samples collected from layers 7y, 10, 12, 13, 14 and 15 by Pontifex and Associates, Kent Town, Adelaide, Australia, which were used to identify mineralogy of grains and sedimentary microstructures indicative of depositional and pedogenic processes (Kemp 2007; van der Meer & Menzies 2011). These slides were also used to confirm sediment composition, grain roundness and sphericity.

Fig. 2. Stratigraphy of each face of the Kelly Hill Cave excavation, Kangaroo Island, South Australia. Three disturbed (1–3) and twelve undisturbed (4–15) sedimentary layers (L) that group into seven units (U) were identified based on sediment colour and texture. These layers were used to guide the excavation. Positions of speleothems are indicated by black symbols. Age (ka) indicates the time over which each unit accumulated based on both U–Th and radiocarbon ages. Full chronological data can be seen in Tables 1, S1 and S2. Dating results suggest a depositional hiatus occurred between accumulation of units 3 and 2 and that unit 2 has been reworked (hatched area). Dashed lines denote a fault line in the sediment; shaded area indicates sediment most heavily influenced by organic carbon-rich drip water; dotted lines indicate stratigraphic boundaries that have been altered by drip water; sc = stream channel with clast of stranded articulated sediment; ob = overburden; Dist. = disturbed layers. This diagram is based on Fig. S2, a composite image of the excavation walls.



Major and trace elemental geochemistry

Each sedimentary layer was geochemically profiled to detect differences in the chemical characteristics that may help identify the surficial sediment source. Oven dried samples were passed through a 2000 µm Endecott sieve to ensure the exclusion of laterite gravel, limestone and bone fragments. Subsamples of the <2000 µm were then pulped using a Rocklabs ring mill. The bulk sediment geochemistry of 16 cave and 6 surface pulp samples were assayed by Acme Analytical Laboratories, Canada, using whole rock Inductively-Coupled Plasma Optical Emission Spectrometry. The analysis reported the weight percent (wt %) of major elemental oxides (Al_2O_3, Fe_2O_3, CaO, MgO, Na_2O, K_2O, MnO, TiO_2, P_2O_5, Cr_2O_3) and concentration (ppm) of trace elements (Ba, Co, Cu, Nb, Ni, Sc, Sr, Y, Zn, Zr and Ce). Loss on ignition (LOI), which measures the combined wt % of organic-matter, hydrated minerals and carbonates in the sediment was also measured and is considered a good estimate of organic carbon content (Craft *et al*. 1991). The wt % of total carbon and sulphur was also determined using the Leco high-frequency induction furnace technique. Linear regression was applied to the geochemical data to assess the nature and extent of major and trace elemental trends within the sediments. They were then compared to relevant published data (Forbes & Bestland 2007).

Results

Kelly Hill Cave and sediment fill

The modern entrance of KHC consists of twin solution pipes of approximately 2–2.5 m diameter located near the crest of Kelly Hill (Fig. 1). The entrances open into a large north–south oriented chamber that is approximately 35 m long, 20 m wide and between 2 and 3 m in height. The floor of the entrance chamber dips 5–10° in all directions from the top of a talus cone beneath the entrances. Two passages lead away from the northeast corner of the entrances chamber. The north passage leads toward the tourist cave whereas the south passage leads to a near-vertical 4 m drop over a rock pile, the bottom of which opens into a large low-roofed east-west oriented chamber that is about 25–30 m long and 10–15 m wide. This chamber is filled with at least 3.5 m of sediments that dip ~3° south away from a narrow (<1 m), now blocked solution pipe through which sediments and bones have entered the chamber. The blocked solution pipe is less than 20 m from the excavation site which is about 25 m beneath the surface and some 30 m west of the modern entrance (Fig. 1).

Stratigraphical description

The KHC sedimentary sequence was excavated in 15 layers, differentiated largely by sediment colour and texture. These layers were later grouped into seven units (Table 2) based on similarity of composition. A fault (Fig. 2), along which very minor displacement has occurred, penetrates all excavated units but does not complicate interpretation of the stratigraphy. All sedimentary units included lateritic clasts ranging between 6 and 12 mm in size. Excavated strata were numbered from the top down but will be described from the bottom up. Differences in layer characteristics, described below, are thought to represent separate episodes or sources of cave sedimentation.

Table 2. (opposite) Colour, bulk grain size distribution and grain size statistics of Kelly Hill Cave stratigraphic layers. Grain size statistics were determined for <1000 µm fraction using Gradistat v8.0. Standard deviation (σ) estimates sorting and represent poorly to very poorly sorted sediments. Skewness (*Sk*) values represent near symmetrical (+0.1 to -0.1), fine skewed (+0.3 to +0.1) and very fine skewed (> +1.0) samples. Kurtosis (*K*) values indicate that most layers are leptokurtic to very leptokurtic but layer 7x is platykurtic and layers 7y and 14 are mesokurtic though *K* may not be accurate for bimodal layers. Quartz grains from all sources were sub-angular to sub-rounded and had low sphericity. D = disturbed.

Layer	Munsell colour	Grain size distribution (weight %)			Grain size statistics for <2000 µm fraction					
(unit)	(dry sediment)	>2000	2000-1000	<1000	Mean	Mode 1	Mode 2	σ	*Sk*	*K*
K Hill Cave strata										
1 (D)	10 YR 4/3 Brown	8.48	1.29	90.23	152.2	257.7	42.76	3.24	-0.499	1.28
2 (D)	10 YR 5/3 Brown	5.04	0.83	94.13	201.2	257.7	-	2.58	-0.418	1.72
3 (D)	10 YR 5/3 Brown	4.34	0.75	94.91	217.9	295.8	-	2.56	-0.403	1.77
4 (1a)	10 YR 4/2 Dark grayish brown	18.08	1.12	80.80	165.3	339.7	37.24	3.95	-0.555	1.38
5 (1a)	10 YR 4/3 Brown	13.94	1.68	84.38	154.7	295.8	37.24	3.43	-0.522	1.33
6 (1a)	10 YR 4/3 Brown	6.84	2.20	90.96	158.3	295.8	-	3.61	-0.582	2.04
7x (1b)	10 YR 4/1 Dark gray	7.64	9.26	83.10	101.0	295.8	32.44	5.06	-0.453	0.89
7y (1b)	7.5 YR 2.5/1 Black	12.86	15.74	71.40	50.48	37.24	295.8	4.62	0.022	1.04
8 (1b)	10 YR 6/4 Light yellowish brown	6.02	0.79	93.19	205.7	257.7	-	2.43	-0.377	1.76
9 (1c)	10 YR 5/2 Grayish brown	13.44	0.77	85.79	191.3	257.7	-	2.81	-0.471	1.91
10 (2)	10 YR 6/4 Light yellowish brown	30.28	0.89	68.83	197.8	257.7	-	2.80	-0.452	1.86
11 (3)	10 YR 6/3 Pale brown	5.75	0.62	93.63	193.2	257.7	-	2.47	-0.388	1.75
12 (4)	10 YR 4/3 Brown	5.10	0.71	94.19	228.2	295.8	-	2.32	-0.329	1.56
13 (5)	10 YR 5/3 Brown	10.42	1.22	88.36	178.4	257.7	-	2.91	-0.467	1.73
14 (6)	7.5 YR 3/4 Dark brown	0.00	0.00	100.00	10.97	14.16	-	4.37	-0.003	0.95
15 (7)	10 YR 6/6 Brownish yellow	3.41	1.63	94.96	231.2	295.8	-	2.98	-0.440	2.08
Kelly Hill surface										
Sample 1	10 YR 4/2 Dark grayish brown	20.32	2.33	77.35	203.7	295.8	-	2.94	-0.455	1.62
Sample 2	10 YR 6/4 Light yellowish brown	35.16	1.28	63.56	230.6	257.7	-	2.23	-0.298	1.54
Sample 3	10 YR 6/4 Light yellowish brown	45.55	1.25	53.20	272.7	295.8	-	2.21	-0.319	1.78
Grassdale surface										
Sample 1	10 YR 5/2 Grayish brown	0.00	0.00	100.00	54.73	295.8	28.25	5.96	-0.199	0.81
Sample 2	10 YR 6/2 Light brownish gray	0.00	0.00	100.00	96.92	295.8	-	4.63	-0.365	0.90
Sample 3	10 YR 6/3 Pale brown	0.00	0.00	100.00	53.89	295.8	21.43	6.19	-0.185	0.79

Layer 15 (unit 7), at the base of the section, is a silty sand that consists of brownish yellow (10 YR 6/6) poorly sorted and packed sub-angular to sub-rounded, course silty medium sand. It lacks charcoal and speleothem and dips ~7° eastward. Only 10 cm of unit 7 has been excavated to date so its full thickness is yet to be determined. Layer 14 (unit 6) is a very thin (2.5–3 cm) dark brown (7.5 YR 3/4) very fine sandy silt, composed of approximately equal proportions of fine to very fine quartz sand and medium to course silt-sized clay pellets. Layer 13 (Unit 5) consists of 13–50 cm thick homogenous poorly sorted and packed brown (10 YR 5/3) sub-angular to sub-rounded, very coarse silty medium sand that appears to have been rapidly deposited. It is superficially similar to unit 7 but lacks the clay pellets observed in layer 15. Layer 12 (unit 4) consists of 13–23 cm thick course to fine, sub-angular to sub-rounded, poorly sorted brown (10 YR 4/3) very coarse silty medium to fine quartz sand. Layer 11 (unit 3) consists of 20–40 cm thick poorly packed and sorted discontinuously inter-bedded pale brown (10 YR 6/3) and brown (10 YR 5/3) very coarse silty fine quartz sand. A very dirty speleothem sheet occurs just above the lower boundary of unit 3, which is capped by another cleaner speleothem. Layer 10 (unit 2) is a 0–16 cm thick wedge of light yellowish brown (10 YR 6/4) poorly sorted and packed coarse silty medium to fine quartz sand. The lower boundary of unit 2 dips ~7° west whereas it’s upper boundary and all overlying sediment has no detectable dip. Layer 10* was not recognised during excavation. It is composed of similar sediments to layer 10 but is more similar to layer 9 in colour. Layer 10* (unit 2) is also capped by a floating speleothem sheet. Layers 9–1 (unit 1) were excavated separately but share very similar physical characteristics (Table 3). They have therefore been grouped together as unit 1 which is 60–75 cm thick.

Table 3. Major and trace geochemical composition of Kelly Hill Cave sedimentary layers and local surface sediments. LOI = loss on ignition; TOT/C = total carbon; TOT/S = total sulphur; D = disturbed sediment.

	Major elements (weight %)											Trace elements (ppm)							Other content		
Layer (Unit)	SiO_2	Al_2O_3	Fe_2O_3	MgO	CaO	Na_2O	K_2O	TiO_2	P_2O_5	MnO	Cr_2O_3	Ba	Ni	Sr	Zr	Y	Nb	Sc	LOI	TOT/C	TOT/S
Kelly Hill Cave strata																					
1 (D)	86.55	5.07	1.65	0.16	0.98	0.25	0.48	0.22	0.04	<0.01	0.016	109	<20	30	310	7	8	4	4.5	0.93	0.03
2 (D)	92.43	2.92	1.09	0.08	0.52	0.11	0.38	0.12	0.02	<0.01	0.019	87	<20	18	112	5	<5	2	2.3	0.42	<0.02
3 (D)	91.69	3.26	1.07	0.09	0.66	0.13	0.43	0.13	0.02	<0.01	0.015	101	<20	21	147	4	5	2	2.5	0.38	<0.02
4 (1a)	86.72	5.11	1.64	0.16	0.95	0.24	0.47	0.22	0.03	<0.01	0.017	110	<20	30	321	7	7	4	4.4	0.82	0.03
5 (1a)	88.90	4.74	1.43	0.12	0.64	0.14	0.44	0.18	0.02	<0.01	0.017	99	<20	23	199	7	5	4	3.3	0.45	<0.02
6 (1a)	91.13	3.73	1.16	0.10	0.53	0.15	0.39	0.17	0.03	<0.01	0.015	96	<20	19	388	7	<5	3	2.5	0.32	<0.02
7x (1b)	77.24	9.03	2.74	0.28	1.96	0.27	0.52	0.36	0.06	<0.01	0.019	110	<20	47	325	13	5	9	7.4	1.62	<0.02
7y (1b)	59.31	13.12	4.07	0.58	2.63	0.54	0.60	0.49	0.12	0.01	0.025	134	25	94	219	21	9	14	18.4	6.18	<0.02
8 (1b)	92.55	2.80	0.89	0.09	0.99	0.11	0.42	0.13	0.03	<0.01	0.016	99	<20	21	251	5	9	2	1.9	0.32	<0.02
9 (1c)	91.31	3.23	1.00	0.10	0.96	0.13	0.45	0.15	0.03	<0.01	0.015	110	<20	22	287	12	<5	2	2.6	0.34	<0.02
10 (2)	91.88	3.40	1.05	0.09	0.47	0.13	0.43	0.16	0.04	<0.01	0.014	99	<20	18	289	6	<5	3	2.3	0.21	<0.02
11 (3)	94.50	2.28	0.71	0.06	0.23	0.09	0.40	0.10	0.02	<0.01	0.012	99	<20	15	111	4	<5	2	1.6	0.16	<0.02
12 (4)	93.49	2.93	0.92	0.09	0.37	0.12	0.47	0.13	0.03	<0.01	0.017	112	<20	20	168	4	<5	2	1.4	0.25	<0.02
13 (5)	91.41	3.04	0.95	0.12	1.06	0.15	0.46	0.15	0.04	<0.01	0.014	111	<20	28	274	6	<5	2	2.5	0.45	<0.02
14 (6)	52.43	22.78	7.08	0.65	0.76	0.61	1.05	0.97	0.16	0.02	0.037	193	40	71	311	36	16	21	13.3	1.34	0.02
15 (7)	94.98	2.40	0.79	0.06	0.17	0.08	0.36	0.11	<0.01	<0.01	0.014	79	<20	12	88	5	<5	2	1.0	0.08	<0.02
Kelly Hill surface																					
Sample 1	83.13	7.24	2.01	0.24	0.39	0.58	1.26	0.60	<0.01	0.02	0.016	327	<20	59	347	18	11	6	4.4	1.33	<0.02
Sample 2	94.26	2.34	0.65	0.05	0.04	0.07	0.44	0.15	<0.01	<0.01	0.013	112	<20	14	626	14	<5	1	1.9	0.50	<0.02
Sample 3	94.02	2.54	0.72	0.04	0.04	0.06	0.42	0.15	<0.01	<0.01	0.016	102	<20	14	421	5	<5	1	1.9	0.60	<0.02
Grassdale surface																					
Sample 1	92.98	2.60	0.84	0.05	0.08	0.06	0.41	0.15	0.01	<0.01	0.013	102	<20	16	506	11	<5	1	2.7	1.22	<0.02
Sample 2	89.30	4.06	0.88	0.09	0.31	0.58	1.00	0.43	0.01	0.01	0.018	303	<20	56	325	13	8	3	3.2	1.35	<0.02
Sample 3	82.07	7.41	2.15	0.25	0.38	0.55	1.22	0.56	0.01	0.01	0.014	309	<20	56	256	18	10	6	5.3	1.31	<0.02

Layers 3–1 appear to have been disturbed prior to excavation and have therefore been excluded from further analysis. Layers 9–4 are composed primarily of very poorly to poorly sorted, medium to fine grained quartz sand that ranges in colour from brown (10 YR 4/3 and 10 YR 5/3) to dark grayish brown (10 YR 4/2) and contains numerous broken straws, pieces of charcoal and much more organic material than any of the underlying units. This unit also includes a black (7.5 YR 2.5/1) load cast-like feature (Fig. 2) that has been strongly influenced by a localised influx of organic carbon and has a comparatively high silt and clay content compared with most other units. A shallow stream channel suggests part of unit 1 has experienced minor low energy hydraulic reworking. However, it is unlikely that such a small-scale channel could cause significant time averaging of sediment borne fossils. Unit 1 includes three floating speleothem sheets which cap layers 7, 5 and 4.

Radiometric dating

Fifteen bone samples were radiocarbon dated (four from Rafter Radiocarbon, 10 from the ANSTO and one from Beta Analytic; Table 1; Fig. 3). At ANSTO, 46 bones were assessed for suitability for radiocarbon dating, 70% were deemed too degraded to process, as indicated by their unacceptable N% values or low collagen yield. As expected, the degree of preservation varied with depth. All bones from layers 3 to 8 provided viable collagen and were dated. Bones from layers 9 and 10 (Fig. 2) exhibited some degradation with 77% of bones tested falling within the acceptable N% range. However, only 17% of bones in layer 11 (Fig. 2) contained datable collagen and all of the 25 bones tested from layers 12 to 15 (Fig. 2) were found to be too degraded for analysis (Table S1).

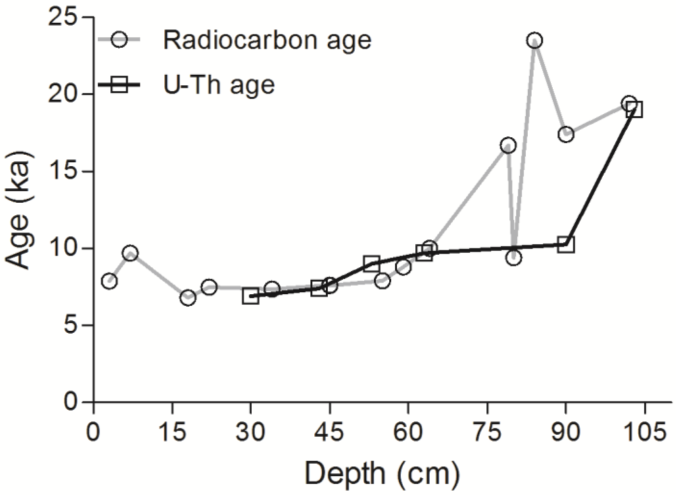


Fig. 3. Plot of radiocarbon and U–Th ages vs. depth below surface of the Kelly Hill Cave excavation, Kangaroo Island, South Australia.

The deepest datable sample (OZN793) has a calibrated radiocarbon age of 19.4 cal. ka BP (layer 11 S3; Table 1), whilst the uppermost (NZA 33933) has a median age of 6.8 cal. ka BP (layer 5; Table 1). Radiocarbon ages for layers 1 and 3 are older than the U–Th age from layer 5 indicating surface disturbance. They are therefore excluded from further analyses. All bone specimens from units7–4 (layers 15–12; Fig. 2) contained little or no nitrogen, indicating collagen degradation, precluding radiocarbon dating (Table S1). Calibrated ages obtained from layers 5 and 6 (Fig. 2; Table 1) indicate a minor stratigraphic age reversal. The calibrated radiocarbon ages obtained from sub-layers 7x and 7y (Fig. 2; Table 1) are the same indicating that despite apparent sedimentological differences, these sub-layers and their contents are approximately contemporaneous and can be combined for the purposes of palaeoenvironmental analysis. Calibrated radiocarbon ages from layer 10 (Fig. 2; Table 1) range between 9.4 and 23.5 cal. ka BP indicating that the layer has been reworked. Radiocarbon age determinations and supporting data are presented in Table S2.

Radiocarbon ages from layers 5 to 9 are essentially in stratigraphic order (Table 1). A small reversal occurs between samples OZN781 (layer 5) and OZN784 (layer 6). However, as the age difference is very small the degree of time averaging and reworking is considered inconsequential. In fact, ages obtained from layers 5 to 9 are so similar that they could be considered a single depositional unit (Unit 1). Ages from layer 10 (Table 1) on the other hand, are significantly out of stratigraphic order. However, C:N ratios and δ^{13}C values for OZO531 and OZO532 indicate that these bones were of acceptable quality for dating (see van Klinken 1999). The ages for OZO531 and OZO532 are both older than the U–Th age for level 11 (Spit 1) suggesting that age reversals seen in the bone radiocarbon ages from layers 10 and 10*are the result of reworking processes operating in the cave. The fact that the bone samples analysed from the deposit have δ^{13}C values that fall into two main groupings according to their radiocarbon age estimates (Table S2) is significant in this context. Bones which return an age of 7 to10 cal. ka BP have δ^{13}C values of between –21.4 to –23.0‰ and bones which date to older than ~17 cal. ka BP have δ^{13}C values of between –17.0 to –17.6‰. It appears therefore that the bones from these two time periods were formed under quite different environmental conditions. Alternatively, the higher δ^{13}C, or greater C4 influence, of the older bones may be interpreted as a decomposition signal. Regardless, both interpretations the δ^{13}C values and radiocarbon age estimates are consistent with the occurrence of reworking in layer 10.

Eight U–Th dates obtained from six speleothems from the KHC excavation yielded ages between 6.9±0.4 ka and 19±1 ka after correction for likely detrital ^{230}Th contents (Table 1). Most speleothems occurred on the upper surface of the layer from which they originate. Age estimates and supporting data are presented in Table S3.

All U–Th ages from the KHC excavation are internally consistent and in correct stratigraphic order within limits of their uncertainties (Table 1), indicating preservation of the primary sedimentary context of the deposit. They generally compare well with the radiocarbon ages but suggest a lengthy hiatus in sedimentation in the terminal Pleistocene.

Sedimentary analyses

Fifteen layers differentiated by sediment colour, which varies from black to light yellowish brown (Table 2), were recognised during excavation. Grain size statistics and bulk sediment grain size compositions show that the majority of the sedimentary layers consist of very poorly sorted, very finely skewed, leptokurtic to very leptokurtic, sub-angular to sub-rounded allochthonous siliciclastic muddy sand to sandy mud (Table 2; Fig. S1).

Particle size analysis of the <1000 µm fraction of sediment shows that except for layer 14, all stratigraphic layers appear weakly bimodally distributed. The primary mode for layers 1-6, 8-13 and 15 occur at ~250 µm and accounts for 7.6–9.4% of the sediment. The secondary mode of these layers occurs at ~37 µm and accounts for 0.6–1.7% of the sediment (see Fig. S1). Sub-layers 7x and 7y have similar mode peaks to other layers but they account for very different quantities of sediment. The primary mode for sub-layer 7x occurs at 295.8 µm accounting for 5.1% of the sediment and the secondary mode occurs at 32.44 µm, accounting for 2.6% of sediment, whereas in sub-layer 7y the primary mode occurs at 37.24 µm accounting for 4.2% of the sediment and the secondary mode occurs at 295.8 µm accounting for 2.5% of the sediment. The sediment distribution curve for layer 14 is unimodal and has a mesokurtic distribution unlike any of the other layers. In addition, sub-layer 7y and layer 14 contain much less quartz than all other layers.

Interspersed between these siliciclastic sediments were six *in situ* speleothems (Fig. 2). Most were deposited at stratigraphic boundaries, indicating periods of low or slower clastic sedimentation, but one (UMD120309-217) incorporated a considerable quantity of sediment suggesting that it was deposited at about the same rate as clastic sedimentation.

Petrographic analysis shows that many quartz grains from layers 13 and 15 are partially coated with clay. Layers 14 and 15, contain bright clay (clay grains oriented such that they pass light under cross polars) that is indicative of post-depositional translocation, probably facilitated by pore water movement through the sediment. Clay coatings were also observed on bones and voids in layers 7y, 12, 14 and 15 (Fig. 4 A, B).

Micro-layering occurs in layers 12, 14 and 15 (Fig. 4C-E). Limestone clasts (≤50 mm) and micrite are rare. Opaline silica was observed in layer 10 (Fig. F). ‘Laterite’ gravel (≤8 mm) was present in all layers and made up the majority of the >2000 µu fraction of the cave sediments (Table 2). ‘Laterite’ was also observed in petrographic slides. In most cases, these clasts appear to be amorphous ferruginous coatings (Fig. 4G) which have accumulated around quartz grains. However, other dark clasts that consist of pieces of charcoal that has been coated in quartz grains and cemented by a clay matrix (Fig. 4H).

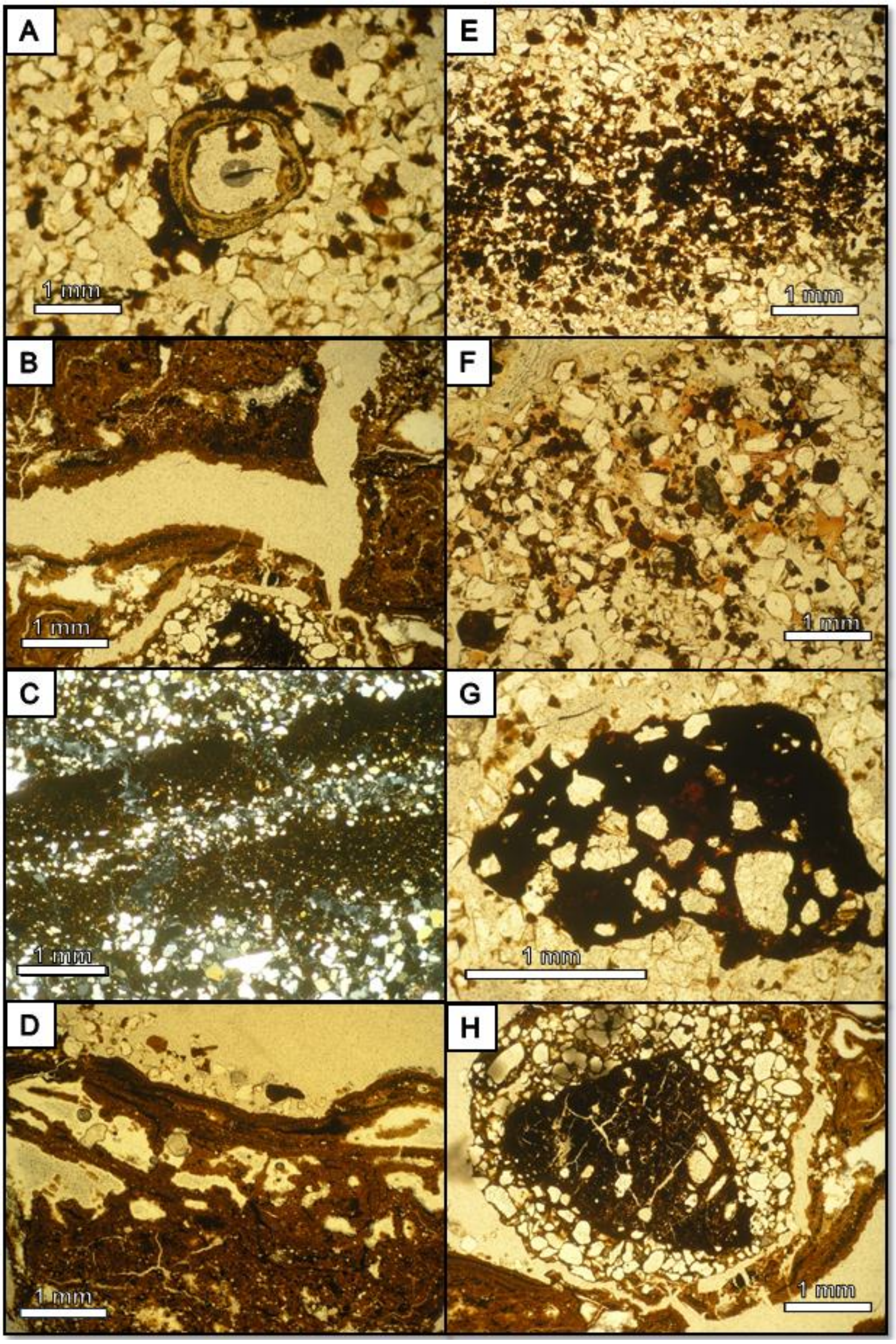


Fig. 4. Photomicrographs from petrographic slides of articulated cave sediments excavated from Kelly Hill Cave, Kangaroo Island, South Australia. A. Cutan development in a hollow bone fragment from layer 15. B. Cutan development in a void from layer 14. C. Micro-layering of dust drapes with aeolian sand from layer 12. D. Micro-layering or possible biofilms from layer 12. E. Micro-layer of clay pellets in layer 15. F. Opaline glass from layer 10. G. ‘Laterite’ clast of ferruginous material seeded on quartz grains from layer 13. H. ‘Laterite’ clast seeded on charcoal and coated in quartz grains and clay from layer 14.

Geochemical analysis

Silica is the most abundant elemental oxide in the sediments, contributing 52.43–94.98 wt% of sediments throughout the deposit (Fig. 5; Table 3) and has a significant negative linear relationship with all major elements and LOI (Fig. 6A-K). Al_2O_3 contents range between 2.28 and 22.78 wt % and LOI accounts for between 1.0 and 18.4 wt%. Fe_2O_3 content is also high relative to other measured major elements, ranging between 0.71 and 7.08 wt%, and has a significant positive linear relationship with Al_2O_3 (Fig. 6L). Al_2O_3 and Fe_2O_3 also have significant positive linear relationships with clay mineral content (Fig. 6M, N). CaO (0.17–2.63 wt%) and P_2O_5 (0.0–0.16 wt%) content appears very low, though both show a significant positive relationship with LOI most likely reflecting their presence in organic matter (Fig. 6 O, P). Na_2O, K_2O and MgO combined account for less than 2% of any sample. Of the trace elements, Zr (88–388 ppm), Ba (79–193 ppm) and Sr (12–94 ppm) are most highly concentrated. Y (4–36 ppm) is present in low concentration and Ni and Nb are barely measurable (Fig. 5). Total carbon content (TOT/C) ranges between 0.08 and 6.18 wt%, and sulphur is barely measurable and does not exceed 0.03 wt% in any sample.

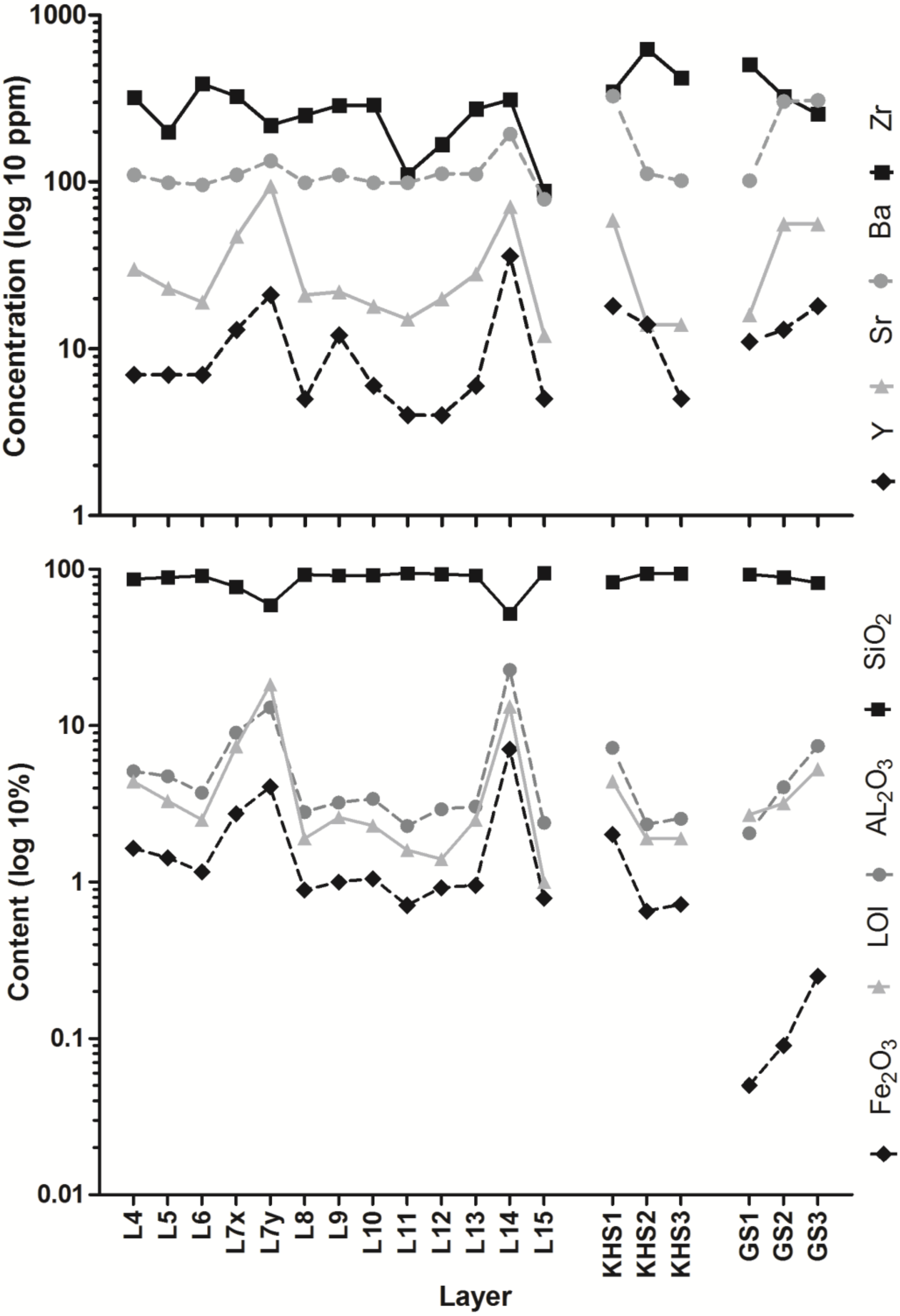


Fig. 5. Major and trace elemental geochemistry of sedimentary layers excavated from Kelly Hill Cave, Kangaroo Island, South Australia.

Discussion

Chronology

There is general agreement between the U–Th and radiocarbon ages from layers 5–9 and layer 11 but age estimates for layers 10 and 10* are inconsistent. Chronological data may be interpreted in three ways:

1. If all of the U–Th dates (Table S3) are considered reliable, three of the radiocarbon ages (OZO531, Beta-320117 and OZO532) must be considered unreliable or reworked. This scenario suggests an extensive depositional hiatus of clastic sedimentation at the excavation site during the Late Pleistocene, near the end of which the speleothem capping Layer 11(UMD120309-311) accumulated 10.25±0.07 ka ago. Deposition of apparently reworked clastic material (layer 10) then occurred, followed by deposition of *in situ* Holocene material in layer 9.
2. The U–Th age UMD120309-311 and radiocarbon ages OZO531 and Beta-320117 are considered unreliable. This scenario suggests continuous clastic deposition with *in situ* Holocene aged material first accumulating in layer 10*.
3. The U–Th age UMD120309-311 and radiocarbon ages NZA 33977 and Beta-320117 are considered unreliable. This scenario also suggests continuous clastic deposition but with *in situ* Holocene aged material first accumulating in layer 9.

Given that i) each of the dated speleothem rafts were excavated *in situ*, most with thin delicate aprons, ii) the U–Th ages are internally consistent, and iii) some of the radiocarbon ages are clearly out of sequence (Fig. 3), it would be difficult to argue that one of the U–Th ages is unreliable without calling them all into question.

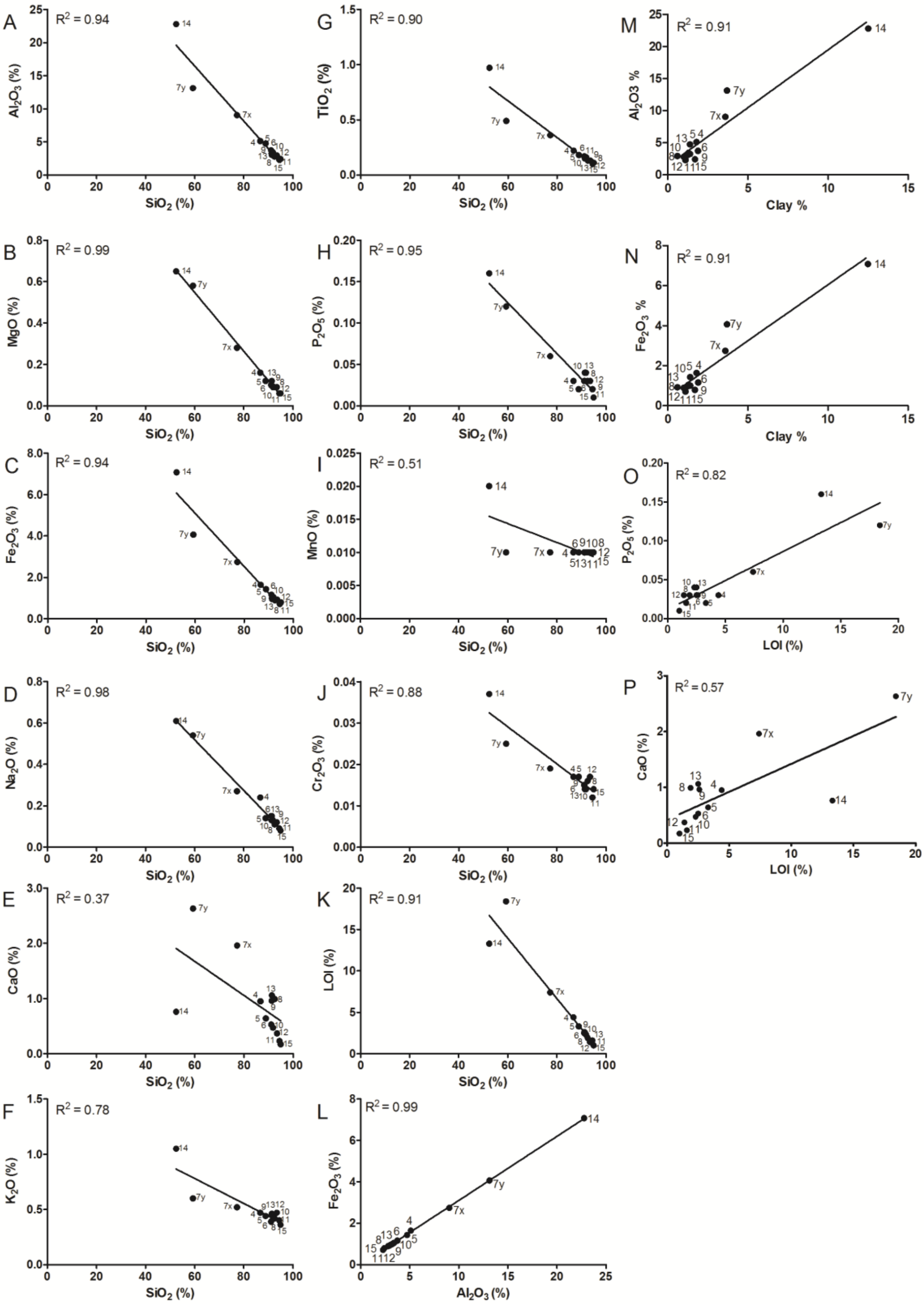


Fig. 6. Linear correlation of major elements and LOI with SiO_2 (A-K), Al_2O_3 with Fe_2O_3 (L) Al_2O_3 and Fe_2O_3 with clay content (M, N) and P_2O_5 and CaO with LOI (O, P) for each sedimentary layer excavated from Kelly Hill Cave, Kangaroo Island, South Australia.

Therefore, the most parsimonious interpretation of the combined chronologies is to accept that the U–Th ages are all reliable and that the sediment and bones that compose layer 10 have been reworked. Due to the absence of charcoal, *in situ* speleothem and poor bone collagen preservation, units 4–7 (layer 11–layer 15) have not been dated. However, *in situ* sthenurine (short-faced) kangaroos occur in unit 7. Sthenurine remains from nearby Black Creek Swamp have been dated to ≥45 ka (Wells *et al*. 2006). Therefore, we tentatively suggest a minimum age of 45 ka be ascribed to unit 7 which in turn suggests that units 6–4 accumulated between 45 and 20 ka ago.

Sedimentary analysis

The vast majority of sediments excavated from KHC share similar physical properties, suggesting they probably originate from a similar parent source, but may have been influenced by varying pedogenic processes. They are also similar to surface sediments collected from the vicinity of the caves now-blocked palaeo-entrance. However, layer 14 and sub-layer 7y are distinctly different in composition. The grain-size distribution of the <1000 µm fraction sampled from layer 14 was much finer than all other layers despite petrographic analysis showing that sediments from layer 14 consist largely of course silt-sized clay pellets. The very fine particle size distribution determined by the Mastersizer suggests that these clay pellets disaggregated in the solution used to measure particle sizes. The texture and composition of sub-layer 7y also differed from the majority of other layers. These sediments have been heavily influenced by local deposition of organic carbon that appears to have been introduced into the cave as particles or colloids suspended or dissolved in vadose drip water. In Podzol soil development, soils rich in quartz can become very acidic and cause organic carbon to be leached from the A horizon and precipitated in the B or C horizons (Urushibara-Yoshino 1996; Sommer *et al*. 2001; Rumpel *et al*. 2002). This process can occurs in quartz rich Bridgewater Formation sediments (Urushibara-Yoshino 1996) but reports of organic carbon deposition in caves due to this process appear to be restricted to speleothem studies (e.g. Dare-Edwards 1984; McTainsh 1989).

Petrographic analysis showed that many quartz grains, bones and/or voids observed in layers 7y, 10, 13, 14 and 15 were coated with clay (Fig. 4 A, B). These clay coats, or cutans, form by the post-depositional illuviation of colloidal clays suspended in pore water moving through the deposit (Fitzsimmons *et al*. 2007; van der Meer & Menzies 2011). Some of the cutans observed were complete and uniform indicating that they had formed *in situ* (Fitzsimmons *et al*. 2007). However, some cutans observed on quartz grains from layers 10, 13 and 15 appeared to be non-uniform or broken, indicating that they have been reworked from a pre-existing soil prior to deposition in the cave (Fig. 4 A). As these relic cutans were not completely destroyed it is thought that they were transported a short distance only (Fitzsimmons *et al*. 2007).

Microstructures observed on petrographic slides indicate that the Late Pleistocene-aged sediments deposited in KHC (layers 15–11) have experienced little reworking. Layer 12 hosts repeatedly inter-bedded silt and sand (Fig. 4 C) that appear to have been deposited by wind and/or gravity. The silt layers, which fill the interstitial space between underlying sand grains but have relatively smooth superior boundaries, resemble dust fall that has draped over the aeolian sands. Much finer laminations were observed in layer 14 which may represent pedogenically redeposited clay or biofilms (Fig. 4 D). In addition, petrographic analysis of layer 15 revealed a clay pellet-rich micro-layer inter-bedded with quartz sand (Fig. 4 E). The clay pellets observed in layer 15 appeared very similar to those seen in layer 14 suggesting they originated from a common source.

Geochemical analysis

The major and trace element values of KHC layers vary within a moderate range. SiO_2 (present as quartz sand) contributes a very large proportion of the siliciclastic sediment in almost all layers. Immobile trace elements such as Zr, Nb and Cr are present in low concentrations (Table 3). Trace elements in dense minerals may be winnowed out of sediments by aeolian transport and parent sediment geochemical signatures can be further diluted by the resulting abundance of fine sediments (Dickson & Scott 1998; McLennan 2001; Forbes & Bestland 2007). Sub-layer 7y and layer 14 are clearly geochemically different to all other layers (Fig. 6) suggesting that they were deposited under conditions that did not occur at any other period during deposition of the KHC sedimentary sequence. Sub-layer 7y and layer 14 are distinguished by high Al_2O_3 and Fe_2O_3 that correlate significantly with low SiO_2 content compared with other layers (Fig. 6). Al and Fe, which are more common in the fine-grained sediment fractions, are also positively correlated (Fig. 6 L) and with the exception of layers 14 and 7, appear to increase with decreasing depth (Table 3). In addition, both Al and Fe correlate positively with clay wt% (Fig. 6 M, N; R^2=0.91 for both elements). As Al and Fe are abundant in clay minerals and iron oxides of fine grain sizes (Sheldon & Tabor 2009), our findings suggest that linear relationships for Al and Fe elements may be directly related to fine sediment content.

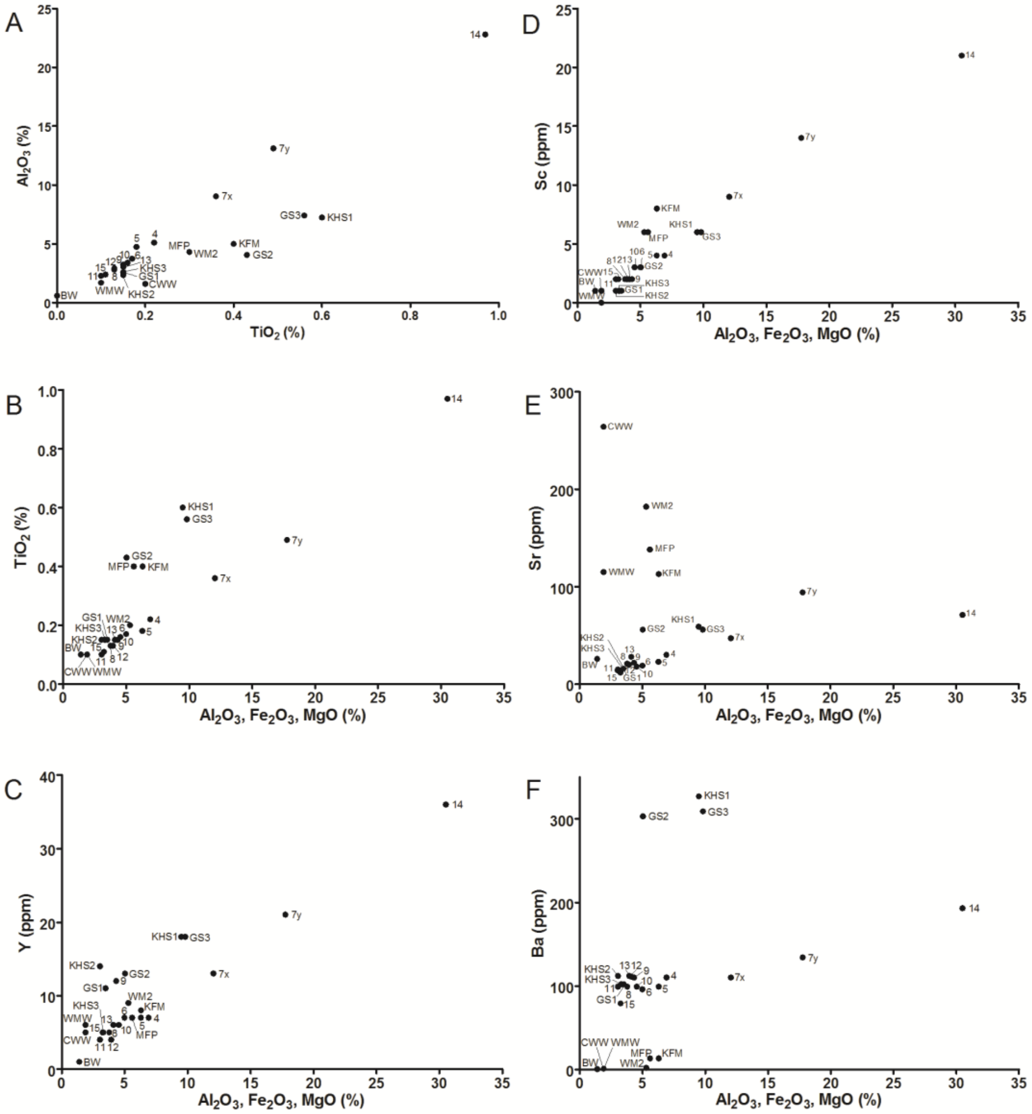


Fig. 7. Comparison of Kelly Hill Cave and regional surficial sediment geochemical composition. A. Al_2O_3 (%) vs. TiO_2 (%). B. TiO_2 (%) vs. combined Al_2O_3, Fe_2O_3 and MgO (%). C. Y ppm vs. combined Al_2O_3, Fe_2O_3 and MgO (%). D. Sc ppm vs. combined Al_2O_3, Fe_2O_3 and MgO (%). E. Sr ppm vs. combined Al_2O_3, Fe_2O_3 and MgO (%). F. Ba ppm vs. combined Al_2O_3, Fe_2O_3 and MgO (%). 4 = KHC layer 4; 5 = KHC layer 5; 6 = KHC layer 6; 7x = KHC sublayer 7x; 7y = KHC sublayer 7y; 8 = KHC layer 8; 9 = KHC layer 9; 10 = KHC layer 10; 11 = KHC layer 11; 12 = KHC layer 12; 13 = KHC layer 13; 14 = KHC layer 14; 15 = KHC layer 15; KHS1 = Kelly Hill surface sample 1; KHS2 = Kelly Hill surface sample 2; KHS3 = Kelly Hill surface sample 3; GS1 = Grassdale surface sample 1; GS2 = Grassdale surface sample 2; GS3 = Grassdale surface sample 3; CWW = Woods Wells Coorong; MFP = Meningie floodplain Coorong; KFM = Kingston floodplain; WM2 = Wellington silty sand (east); WMW = Wellington silty sand (west); BW = Bridgewater Formation (after Forbes & Bestland 2007).

CaO has a significant positive relationship with LOI (Fig. 6 P) and is most concentrated in sub-layers 7x and 7y which have been influenced by exogenic organic carbon. $CaCO_3$ was no more abundant in these sub-layers than any other layer, suggesting that CaO is related to organic content. The very low CaO content of the KHC sediments can be attributed to weathering and destruction of calcareous sand grains during aeolian transport to the cave area, followed by dissolution within the cave system itself (Forbes & Bestland 2007). Geochemical profiles of KHC strata were compared with local and mainland sediments (Fig. 7). Strong similarities were observed between the KHC strata and the Kelly Hill surface samples particularly for Al_2O_3 vs. TiO_2 and TiO_2 vs. combined Al_2O_3, Fe_2O_3 and MgO (%) (Fig. 7 A, B).

Trace element concentrations plotted against combined Al_2O_3, Fe_2O_3 and MgO% (Fig. 7 C-F) add further support to the similarity of KHC and the Kelly Hill surface sediments, particularly Ba concentration (Fig. 7 F), which shows KHC strata grouping with several of the KI surface samples to the total exclusion of all mainland samples. These results indicate that the KHC sediments have been reworked into the cave from local sources, probably by wind. Similarities between KHC layers and some mainland samples most likely indicate that they were deposited from the same parent source rather than Kelly Hill sediments being reworked from mainland sediments.

Palaeoenvironmental context

The age of layer 15 (unit 7) is presently unknown due to the absence of charcoal and speleothem and poor bone collagen preservation. However, the presence of *in situ* associated megafauna specimens suggest it is probably of Late Pleistocene age. Petrographic analysis revealed micro-layers of course silt sized clay pellets (Fig. 4 E) and broken or relic clay cutans on quartz grains which indicate that the sediments that make up unit 7 were eroded from an existing soil or playa-lunette system. Geochemical analysis indicates that unit 7 consists primarily of SiO_2 and contains little organic matter. These characteristics are consistent with the layers' expected age and correlate with drier, windier conditions and diminished vegetation cover of the Late Pleistocene. Retention of the very small particle-size fraction in these sediments indicates aeolian and/or gravitational, rather than hydraulic, deposition.

Almost half of the grains that make up layer 14 (unit 6) consisted of course silt-sized clay pellets which are typically associated with desiccation and erosion of playa lake surfaces by strong winds (Bowler 1973, 1976; De Deckker 1988; Fitzsimmons *et al*. 2007). The abundance of clay pellets in this layer suggests that playa lakes probably occurred west of KI on the exposed continental-shelf during the Late Pleistocene. Alternatively, they may represent exposure and erosion of fine-grained terrigenous sediments deposited on the continental-shelf by the Palaeo-Murray River. Geochemically this layer is distinctly different to the under- and over-lying sediments (Fig. 6). It contains much less SiO_2 and is enriched in AlO_2 and Fe_2O_3, reflecting its high silt and clay content (Fig. 5). Petrographic analysis of this layer revealed fine laminations parallel with the bedding plain (Fig. 4 D), clay cutans coating voids (Fig. 4 B) and structures that are interpreted as fine-grained lateritic gravel (Fig. 4 G, H). During excavation, these sediments were found to have been deposited around a delicate and largely undamaged skull of a Toolache wallaby (*Macropus greyi*; see SI), parts of which rested in the under- and over-lying sediments. This provides additional support for low-energy, aeolian deposition within the cave and is consistent with the prevailing strong winds that are known to have occurred during the Late Pleistocene. Though this layer is yet to be dated, it is thought to be approximately 40 ka old based on megafauna remains in unit 7. The sedimentary and geochemical characteristics of unit 6 suggest that it is the product of a unique depositional environment that did not occur at any other period during deposition of the KHC sedimentary sequence.

Sediments from layer 13 (unit 5) are superficially similar to unit 7 sediments but differ in colour and lack clay pellets. Partial cutans were observed on some grains from unit (Fig. 4 G) but it is not clear whether they represent features preserved from an eroded pre-existing soil or an early stage of *in situ* pedogenesis. Geochemical and physical similarities between units 5 and 7 suggest that they may originate from similar parent sediments.

Layer 12 (unit 4) is compositionally and geochemically similar to units 7 and 5. Macro-stratigraphy (Fig. 2) suggests that this layer was deposited under turbulent conditions. However, petrographic analysis of articulated sediment shows distinct alternating sand and silt micro-layers (Fig. 4 C). The preservation of sharp contacts between the silt and overlying sand layers indicate that the sands were deposited under very low-energy aeolian conditions and suffered minimal subsequent disturbance. As in underlying layers, bone collagen is poorly preserved, probably due to digenesis rather than excessive age, and is therefore unsuitable for radiocarbon dating. Consequently, this layer is yet to be dated but is probably around 30–20 ka old.

Layer 11 (unit 3) is the deepest stratum in which bone collagen preservation has been sufficient for radiocarbon dating. Bone from within the unit and speleothem deposited near its lower boundary are both ~19 ka old, indicating that unit 3 accumulated during the LGM. However, speleothem deposited on the upper boundary of unit 3 was dated ~10 ka old (Table 1; Table S3) suggesting a depositional hiatus during the late LGM, probably caused by a blockage of the entrance solution pipe or chamber by clastic sediments.

Radiocarbon dates (Table 1; Table S3) indicate that the bones and sediments that make up layer 10 and 10* (unit 2) have been reworked, probably when the entrance blockage suggested by the age of speleothem capping unit 3 was released. This is further supported by the absence of micro-layering and pedogenic structures observed in other units. Relic clay cutans were rare in unit 2, but *in situ* pedogenically deposited opaline glass was observed in layer 10* indicating pore water movement occurred after these sediments were deposited. In some cases the opaline silicate had been deposited over relic clay cutans (Fig. 4 F), indicating that unit 2 was reworked from a pre-existing soil.

Based on sediment colour, texture and age, layers 9–1 were excavated separately. However, they share very similar physical characteristics (Table 3) and were deposited over a short time period (Fig. 3; Tables S1, S2) which indicate that these strata accumulated during the Holocene between ~10.0 ka and ~7.0 ka ago (Table 1). Therefore, they have been grouped together as unit 1. Layers 9–4 are composed primarily of medium to fine quartz sand, but compared with Late Pleistocene strata, generally have lower SiO_2 content. The colour of unit 1 sediments has been strongly influenced by localised admixture of organic carbon. Petrographic analysis of sub-layer 7y revealed abundant silt-sized opaque particles, identified as organic matter, which is thought to have been transported into the cave as particles or colloids suspended or dissolved in vadose drip water (Fig. 2). Sediments most affected by this process (represented in the results by sub-layer 7y) have a much larger silt and clay content than less affected adjacent sediment (Fig. S1) and very high LOI (18.4% compared with an average of 4.5% for all layers). A load-cast like structure and deformation of adjacent layers can be seen at the suspected drip-point, indicating that the sediment was very wet at the time of deposition (see shaded area in Fig. 2). Minor hydraulic reworking has also influenced unit 1 suggesting higher effective precipitation occurred during the Holocene. A shallow channel structure has cut through layers 3–4. However, a stranded clast of articulated sediment which occurs in a stream channel (sc in Fig. 2) suggests very low energy reworking. These sedimentary characteristics are consistent with the warmer, wetter conditions that prevailed during the Holocene (e. g. White 1994; Forbes *et al*. 2007). Higher LOI values indicate that greater organic content which correlates with the increased vegetation density known to have prevailed during the Holocene. The abundance of organic carbon transported into the cave via drip water also indicates higher effective precipitation. Organic carbon is frequently dissolved from soil A horizons by mildly acidic water and usually re-precipitates in B horizons (Sommer *et al*. 2001; Rumpel *et al*. 2002). This phenomenon has been previously noted in caves (e.g. Saiz-Jimenez & Hermosin 1999; Simon *et al*. 2007) but is usually restricted to chemical (i. e., speleothem) rather than clastic sediments and has not previously been observed to the extent reported here. Sediment deposition ceased around 7 ka ago, probably when the solution pipe entrance became blocked.

Gingele *et al*. (2007) reconstructed late Quaternary palaeoclimatic change in southeastern Australia using multiple climate proxies from a deep-sea core collected south of southwestern KI. Between 17 and 13.5 ka ago, Gingele *et al*. (2007) reported fluvial clays derived from the combined Murray and Darling River catchment dominated the core sediments, indicating strong deglaciation outflow from the Murray-Darling Basin. From 13.5 ka ago to present sediments began to change from fluvial to aeolian deposition, indicating a trend towards more arid conditions and strengthening westerly winds on the adjacent mainland during the Holocene. This trend was punctuated by two periods of fluvial sedimentation derived from the Murray catchment between 13.5–11.5 and 9.5–7.5 ka ago, indicating more humid conditions in the southern part of the Murray-Darling Basin. Aeolian dust deposition increased between 7.5–5 ka ago then persisted until the present, but peaking about 1.5 ka ago. This record compares well with palaeoclimatic interpretations of Lake Keilambete (Bowler 1981; De Deckker 1982; Chivas *et al*. 1993) and Blue Lake (Stanley & De Deckker 2002).

Palynological records from southeastern Australia and KI have been extensively investigated (Dodson 1974, 1975, 1977, 2001; Dodson & Wilson 1975; Clark 1976; G. Hope *et al.* 1977; Clark & Lampert 1981; Singh *et al.* 1981; Edeny *et al*. 1990; Kershaw *et al.* 1991; D’Costa & Kershaw 1995; Harle 1997; Harle *et al*. 1999; Bickford and Gell 2005; Cook 2009). These studies generally agree that about 50 ka ago, the vegetation of southeastern Australia changed from *Eucalyptus* forest with heath understorey to open *Eucalyptus* woodland with heath and grass understorey or open grassland-steppe. 25–12 ka ago woodlands become more open with *Casuarina* and *Banksia* species becoming more prominent. Between 12 ka and the present, closed *Casuarina*/*Eucalyptus* woodlands predominated. These vegetation changes reflect the overall trend that south-eastern Australia experienced a drier and more seasonal climate during the Quaternary (Kershaw 1995; Kershaw *et al*. 1991).

The KHC sedimentary sequence correlates with the Late Pleistocene environmental changes identified by Gingele *et al*. (2007) and mainland pollen records. However, KHC's Holocene aged sediments contain more organic material and evidence of stream channels, both of which suggest higher effective precipitation occurred on KI at that time. While the terrigenous sediment core studied by Gingele *et al*. (2007) was collected proximal to the Murray Canyons south of KI, the sediment that they studies originated from the Murray-Darling Basin. The increase in aeolian dust reported by Gingele *et al*. (2007) was deposited in the Murray-Darling catchment by strengthening westerly winds blowing across the continent. These winds would have approached KI from the Southern Ocean, accumulating more moisture than the continental winds, thus increasing the relative humidity if not precipitation, on KI during the Holocene.

Comparison with mainland cave and surficial sediments

Southeastern Australian Late Pleistocene and Holocene cave sediment accumulations have been described from the Lower Glenelg region (Kos 2001) and the Naracoorte Caves World Heritage Area (NCWHA; McDowell 2001; Pate *et al*. 2002, 2006; Forbes & Bestland 2007; Forbes *et al*. 2007; Darrénougué *et al*. 2009, Macken *et al*. in press). As in KHC, many of these records have substantial depositional hiatuses but still provide an excellent opportunity to compare cave sedimentary records on a more regional scale.

Forbes *et al*. (2007) and Forbes & Bestland (2007) categorised three sediment types from NCWHA cave fills that accumulated during the Late Pleistocene and Holocene. Typically, Holocene sediments were characterised by organic-rich, brown sandy silt, LGM sediments were typified by pale quartz sands with little organic content, and Late Pleistocene sediments were typified by reddish-brown sandy silt. These sediment categories appear to be generally repeated across southeastern Australia. Kos (2001) reports Holocene-aged organic-rich black to brown sands and

Late Pleistocene-aged orange-brown sands from McEachern's Deathtrap Cave. McDowell (2001) and Forbes & Bestland (2007) observed all three sediment types in Robertson and Wet Caves, and Darrénougué *et al*. (2009) observed LGM-aged homogeneous light brown quartz sands and Late Pleistocene-aged reddish-brown sandy clays in Blanche Cave.

These sedimentary records correlate well with data reported here, though KHC appears to lack the reddish brown sandy silts that typify late Pleistocene sediments in the NCWHA and Lower Glenelg region. Mee *et al*. (2004) determined that the red-brown earth or terra rossa sediments found in the NCWHA were derived largely from weathering products of Kanmantoo metasediments outcrops on KI and Fleurieu Peninsula. Terra rossa-like sediments have not yet been encountered in KHC, but may occur in deeper sediments not yet excavated.

The grain size distribution of sediments excavated from KHC also share similarities with NCWHA cave fills, all suggesting aeolian origin. Geochemical characteristics of KHC strata, Kelly Hill, and mainland surficial sediments from Woods Wells Coorong, west-bank Wellington silty sands and Bridgewater Formation sediments are also similar (Fig. 7).Sub-layer 7y and to a lesser extent 7x are similar to Meningie and Kingston floodplain sediments (Fig. 7). However, sediments from layer 14 are unique (Figs 5, 6). The extent of similarities between the sediments discussed above suggests that the majority of Late Pleistocene- and Holocene-aged southeastern Australian cave fills were deposited by widespread depositional processes. However, the distinctive characteristics of layer 14 and sub-layer 7y also demonstrate that more local processes can also have a very strong effect on cave sedimentation.

Conclusions

The chronology of the upper 1.5 m of the KHC excavation has been established using radiocarbon dating of bone and Uranium series dating of speleothems. Our interpretation of the chronology indicates that the sedimentary sequence was deposited during the Late Pleistocene (including part of the LGM) to mid-Holocene. However, the lack of datable material and degradation of bone collagen in layers 15–12 highlights the need for further chronological investigation, perhaps using optically stimulated luminescence.

Six sedimentary units made up of 12 *in situ* sedimentary layers were identified in the excavation, most of which are light to dark brown, fine grained and can be broadly classified as silty sands. Dating and petrographic analysis of micro-stratigraphic features indicate that apart from layer 10, the sedimentary sequence has experienced minimal reworking. Geochemical analyses indicate that the silts and fine sands were probably derived from Bridgewater Formation parent sediments whilst the presence of clay pellets suggest that during the Late Pleistocene playa lakes or desiccation and erosion of Palaeo-Murray River sediments may have occurred on the exposed continental-shelf south of KI. The ultimate source of the sediments deposited in KHC remains unknown, but they share broad similarities with Late Pleistocene- and Holocene-aged sediments deposited in other southeastern Australian caves. Furthermore, they correlate well with the environmental conditions that are thought to have occurred when the sediments were deposited. This analysis provides a robust chronological and palaeoenvironmental framework for the fossiliferous sedimentary accumulation of KHC. However, further research is required to establish the age of deeper sediments and investigate changes in the fossil assemblages associated with the sedimentary units identified.

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Supplimentary Information

Fig. S1 (opposite). Particle size distributions for each undisturbed sedimentary layer excavated from Kelly Hill Cave and surface sediments from Kelly Hill and Grassdale, Kangaroo Island.

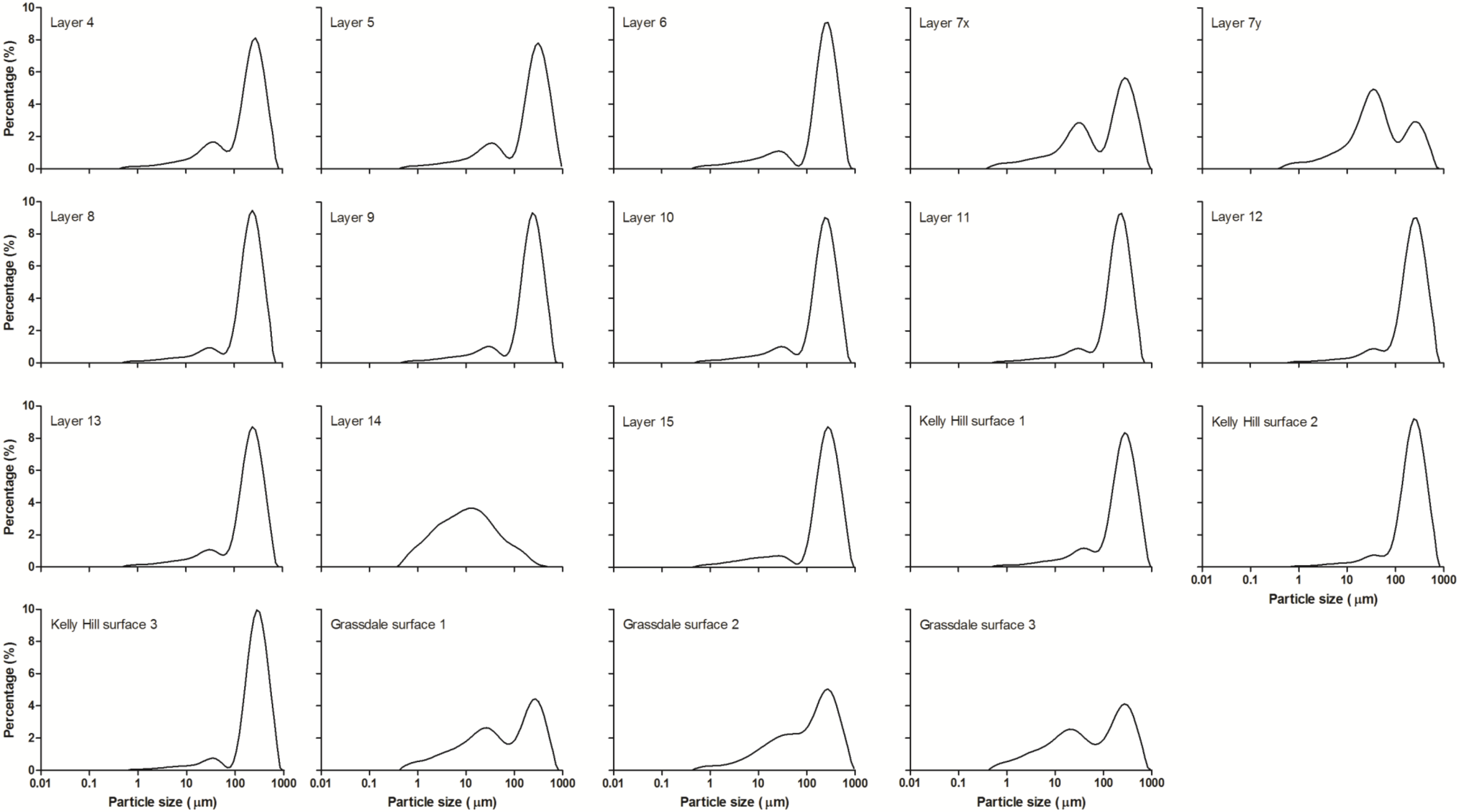
Layer 4
Layer 5
Layer 6
Layer 7x
Layer 7y
Layer 8
Layer 9
Layer 10
Layer 11
Layer 12
Layer 13
Layer 14
Layer 15
Kelly Hill surface 1
Kelly Hill surface 2
Kelly Hill surface 3
Grassdale surface 1
Grassdale surface 2
Grassdale surface 3
Percentage (%)
0
2
4
6
8
10
0.01
0.1
1
10
100
1000
Particle size (μm)

Fig. S2. Composite image of the stratigraphy of each face of the Kelly Hill Cave excavation upon which Fig. 2 was based (scale in the NW face is 0.8 m and 1.0 m in all other faces, each face is 2 m wide).

Table S1. Summary of bone sample quality of all bones analysed from the Kelly Hill Cave excavation by the Australian Nuclear Science and Technology Organisation.

Sample	Layer (Unit)	N% of Bone	Collagen %	C:N (atomic)
OZN779	3 (D)	2.1	4.8	3.4
OZN781	5 (1a)	0.9	0.8	3.3
OZN784	6 (1a)	1.8	2.0	3.2
OZN786	7 (1b)	1.5	3.3	3.4
OZN787	7 (1b)	1.6	3.9	3.3
OZN788	8 (1b)	1.9	0.7	3.4
OZN792	9 (1c)	0.9	0.0	-
OZO526	9 (1c)	0.9	-	-
OZO527	9 (1c)	<0.1	-	-
OZO528	9 (1c)	1.7	4.0	3.2
OZO529	10 (2)	0.2	-	-
OZO530	10 (2)	0.3	-	-
OZO531	10 (2)	1.0	2.2	3.5
OZO532	10 (2)	0.5	0.7	3.5
OZO533	10 (2)	<0.1	-	-
OZN793	11 (3)	2.2	1.7	3.2
OZO744	11 (3)	<0.1	-	-
OZO745	11 (3)	<0.1	-	-
OZO746	11 (3)	<0.1	-	-
OZO747	11 (3)	<0.1	-	-
OZO748	11 (3)	<0.1	-	-
OZO534	12 (4)	<0.1	-	-
OZO535	12 (4)	<0.1	-	-
OZO536	12 (4)	0.2	0.0	-
OZO537	12 (4)	<0.1	-	-
OZO749	12 (4)	<0.1	-	-
OZO750	12 (4)	<0.1	-	-
OZO751	12 (4)	<0.1	-	-
OZN797	13 (5)	<0.1	-	-
OZN798	13 (5)	<0.1	-	-
OZN799	13 (5)	<0.1	-	-
OZN800	13 (5)	<0.1	-	
OZO752	13 (5)	<0.1	-	-
OZO753	13 (5)	<0.1	-	-
OZO754	13 (5)	<0.1	-	-
OZO755	13 (5)	<0.1	-	-
OZO469	14 (6)	<0.1	-	-
OZO470	14 (6)	<0.1	-	-
OZO471	14 (6)	<0.1	-	-
OZO472	14 (6)	<0.1	-	-
OZO473	14 (6)	<0.1	-	-
OZN801	15 (7)	<0.1	-	-
OZN802	15 (7)	<0.1	-	-
OZN803	15 (7)	<0.1	-	-
OZO467	15 (7)	<0.1	-	-
OZO474	15 (7)	<0.1	-	-

Table S2. Radiocarbon results and age estimates of bones dated from the Kelly Hill Cave (5K1) excavation. OZ = ANSTO lab code, NZA = Rafter Radiocarbon lab code, Beta = Beta Analytic lab code, D = disturbed sediment.

Lab Code	Layer (spit)	Unit	C:N (atomic)	$\delta^{13}C$ (‰)	^{14}C age ka BP	Calibrated age cal. ka BP[1]
NZA 33928	1(S1)	D	-	-22.6	7.12 ± 0.04	7.97-7.80 (95.4%)
OZN779	3(S1)	D	3.4	-21.4	8.79 ± 0.05	9.90-9.55 (95.4%)
NZA 33933	5(S1)	1a	-	-22.6	6.03 ± 0.04	6.94-6.68 (95.4%)
OZN781	5(S1)	1a	3.3	-22.9	6.6 ± 0.04	7.57-7.43 (95.4%)
OZN784	6(S1)	1a	3.2	-21.8	6.51 ± 0.05	7.44-7.27 (95.4%)
OZN786	7x(S1)	1b	3.4	-21.8	6.83 ± 0.05	7.69-7.56 (93.2%) 7.54-7.52 (2.2%)
OZN787	7y(S1)	1b	3.3	-23.0	6.79 ± 0.05	7.68-7.50 (95.4%)
OZN788	8(S1)	1b	3.4	-21.8	7.16 ± 0.06	8.04-7.79 (95.4%)
NZA 33932	8(S2)	1b	-	-22.6	7.98 ± 0.04	8.98-8.60 (95.0%)
OZO528	9(S1)	1c	3.2	-22.7	8.97 ± 0.05	10.21-9.79 (95.4%)
OZO531	10(S1)	2	3.5	-21.8	13.58 ± 0.07	16.94-16.48 (95.4%)
NZA 33977	10(S2)	2	-	-22.0	8.41 ± 0.05	9.49-9.25 (93.8%) 9.17-9.15 (1.6%)
Beta-320117	10(S2)	2	-	-17.6	19.61 ± 0.08	23.65-23.33 (95%)
OZO532	10(S3)	2	3.5	-17.5	14.30 ± 0.08	17.75-17.03 (95.4%)
OZN793	11(S3)	3	3.2	-17.0	16.28 ± 0.08	19.81-19.72 (4.1%) 19.59-19.24 (85.4%) 19.10-18.95 (5.9%)

[1] Calibrated age ranges and corresponding probability distribution function area percentages after projection of radiocarbon measurements onto calibration curves using the OxCal 4.1 programme (Bronk Ramsay 2009). Radiocarbon ages <11.0 cal. ka BP were calibrated using the SHCal04 calibration curve (McCormac *et al*. 2004). Radiocarbon ages >11.0 cal. ka BP were calibrated using the IntCal09 calibration curve (Reimer *et al*. (2009).

Table S3. U and Th results and ages estimates of speleothems from the Kelly Hill Cave (5K1) excavation and nearby chamber in Kelly Hill Caves. UMD = University of Melbourne lab code, KH SC = ANU lab code.

Lab Coe	Layer (spit)	Unit	U conc. (ppb)	$^{230}Th/^{232}Th^{1}$	$^{230}Th/^{238}U$	$^{234}U/^{238}U$	Age^{2} (ka)	Age$_{corr.}^{3}$ (ka)	$^{234}U/^{238}U_{corr.\ initial}$
UMD120309-215	5(S3)	1a	80	7	0.070 ± 0.001	1.077 ± 0.003	7.29 ± 0.08	6.9 ± 0.4	1.099 ± 0.003
UMD120309-217	6(S1)	1a	90	9	0.073 ± 0.001	1.079 ± 0.003	7.69 ± 0.05	7.4 ± 0.3	1.102 ± 0.003
UMD120309-225	8(S1)^{T}	1b	120	7	0.073 ± 0.001	1.074 ± 0.003	7.7 ± 0.1	7.3 ± 0.5	1.097 ± 0.003
UMD120309-226	8(S1)^{B}	1b	70	3	0.091 ± 0.003	1.065 ± 0.005	9.7 ± 0.3	9 ± 1	1.091 ± 0.006
UMD120309-242	9(S1)^{T}	1c	60	11	0.105 ± 0.002	1.077 ± 0.003	11.2 ± 0.2	10.8 ± 0.5	1.110 ± 0.004
UMD120309-302	9(S1)^{B}	1c	130	9	0.096 ± 0.001	1.085 ± 0.003	10.10 ± 0.07	9.69 ± 0.41	1.116 ± 0.003
UMD120309-311	11(S1)	3	260	40	0.0997 ± 0.0008	1.102 ± 0.002	10.34 ± 0.03	10.25 ± 0.07	1.134 ± 0.003
UMD120309-312	11(S5)	3	8	6	0.181 ± 0.002	1.094 ± 0.003	19.7 ± 0.2	19 ± 1	1.152 ± 0.005
KH SC S-1a	–	–	120	0.4	0.006 ± 0.001	1.0515 ± 0.0007	0.62 ± 0.03	–	–

[1.] All U and Th ratios are given as activity ratios. [2.] Ages calculated using the half-lives for ^{230}Th (75.69±0.023 ka) and ^{234}U (245.25±0.049 ka) of Cheng *et al*. (2000). [3.] Corrections for detrital ^{230}Th made using $^{230}Th/^{232}Th_{initial}$ = 0.4 ± 0.4 estimated from modern stalagmite sample KH SC S-1a. ^{T} = tip and ^{B} = base of stalagmite. Spits are 5 cm sections of sediment excavated within stratigraphic layers.

CHAPTER 7

The effects of Late Quaternary environmental change and isolation on the non-volant mammals of a large Australian land-bridge island

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Context

This chapter presents a detailed analysis of the late Pleistocene–Holocene non-volant mammals of Kangaroo Island and focuses on their responses to the Last Glacial Maximum and isolation due to sea level rise. The excavated fossil assemblage also includes amphibians, reptiles and birds. These taxa are much less abundant in the assemblage than mammals and will be investigated in future research.

Statement of authorship

I collected, prepared, identified and analysed most of the material examined in this chapter (with additional support from those noted in the Acknowledgements). I supervised volunteers who assisted in excavation and preparation of fossil specimens. I prepared land-snail shells for stable isotope analysis. I prepared the original and final manuscript for publication.

Gavin J. Prideaux provided guidance and advice, contributed to identification of small macropodids, commented on the draft manuscript and contributed to the discussion.

Alexander Baynes provided advice on data analysis, commented on the draft manuscript and contributed to the discussion.

Linda K. Ayliffe calibrated and interpreted the U–Th dates, provided guidance for preparation, analysis and interpretation of land-snail shells for stable isotope analysis, commented on the draft manuscript and contributed to the discussion.

Fiona Bertuch conducted AMS radiocarbon dating and commented on the draft manuscript.

John C. Hellstrom conducted the U–Th dating.

Geraldine E. Jacobsen coordinated AMS radiocarbon dating and commented on the draft manuscript.

The effects of late Quaternary environmental change and isolation on the non-volant mammals of a large Australian land-bridge island

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Keywords: Faunal change; Kangaroo Island; Murray-Mallee; Pleistocene; LGM; Holocene

Abstract

Late Quaternary climatic changes had dramatic effects on terrestrial landscapes and biotas. Impacts were likely especially intense on land-bridge islands where isolation due to rising sea levels greatly reduced potential for immigration and colonisation. To date, however, studies of such islands have only been able to infer changes based largely on modern diversity due to the lack of long term fossil records. Here we examine late Quaternary non-volant mammal occurrence and variability in a cave assemblage on Kangaroo Island (KI), South Australia. Total species richness, evenness and composition did not vary greatly with time, but relative abundances of ecologically divergent species did. The relative abundance of several heath species declined from the Late Pleistocene into the Holocene, arid-zone species numbers peaked around the last glacial maximum (LGM) and the relative abundance of mallee woodland species increased during the Holocene. These patterns, supported by stable isotope and sedimentary records, correlate with the climatic transition from the relatively cool, dry Late Pleistocene, through the arid LGM and into the relatively warmer, wetter Holocene. Few mammals disappeared during the LGM, but several disappeared after KI was isolated by early Holocene sea-level rise. This supports an emerging view that southern Australia's native fauna is resilient to climate change, but that effects of isolation can be severe, even on islands as large as KI. This suggests that most nature reserves are nowhere near large enough highlighting the importance of maintaining native mammal populations outside the reserve system to allow species dispersal and migration with habitat.

Introduction

Many studies of island populations show that they tend to have different evolutionary trajectories from their mainland counterparts and often evolve more rapidly (MacArthur and Wilson 1963, 1967; Adler and Levins 1994; Berry 1996; Lomolino 2005; Raia and Meiri 2006). Islands also differ at the community ecological level, and the positive relationship between increasing island area and species richness has been so widely documented that it is almost considered a universal ecological 'law' (e.g., Ricklefs and Lovette 1999; Leigh *et al*. 2007). From a conservation perspective, islands can provide refugia for species extirpated from the mainland (e.g., Vartanyan *et al*. 1993; Brenchley and Harper 1998; Lister 2004; Turney *et al*.

2008; van der Geer 2010). However, island populations are often more susceptible to reduced genetic diversity or exotic competitors and predators (Kadmon and Pulliam 1993; Johnson *et al*. 2000; Brown *et al*. 2001; Magurran and Henderson 2003; Mills *et al*. 2004). Island isolates have no or highly reduced capacity to migrate with their ecological niche as it shifts with climate change, a situation often paralleled on the mainland by populations restricted to habitat “islands”, e.g., nature reserves and artificial islands within reservoirs (Newmark 1987; Laurance 1991; Foufopoulos *et al*. 2011).

Several Australian mammals currently persist only on islands e.g. *Bettongia lesueur, Perameles bougainville, Lagostrophus fasciatus* and *Leporillus conditor* (van Dyck and Strahan 2008). In addition, Turney *et al*. (2008) reported that several species of megafauna survived on Tasmania up to 6 thousand years (kyr) after their mainland extinction. Islands are therefore of enormous conservation importance for Australian native mammals (e.g. Burbidge *et al*. 1997, Burbidge and Manly 2002; SI Appendix). Consequently, it is important that we understand how mammals have responded to environmental change and isolation on islands in the past. Land-bridge islands are of particular interest, being isolated from adjacent mainland areas when sea levels are higher during warm climatic phases and connected to them during cooler phases (Diamond 1975; Lomolino 1984, 1986). This makes them excellent potential analogues for assessing long-term effects of anthropogenic habitat fragmentation.

The equilibrium theory of island biogeography predicts that land-bridge island faunas, which support diverse fauna after initial isolation, suffer elevated selection pressures and extinction rates. It further predicts that species with the highest resource needs should be affected first (MacArthur and Wilson 1963, 1967). Experimental land-bridge island work has centred on short-term studies after recent fragmentation, which can only track initial adjustments (e.g., Kadmon and Pulliam 1993; Cosson *et al*. 1999; Foufopoulos and Ives 1999; Terborgh *et al*. 2001; Lambert *et al*. 2003). Other land-bridge island studies to date have shown, or predicted based on mainland fauna, only what species lived on islands *at some point* in the past and what inhabits them now (e.g., Heaney 1984; Lawlor 1986; Gurd 2006; Okie and Brown 2009).

KI, Australia's third largest Island, has an area of 4405 km^2 and lies off the coast of South Australia on a broad expanse of continental-shelf that extends about 100 km south of Eyre, Yorke and Fleurieu Peninsulas (Lampert 1981; Twidale and Bourne 2002; Fig. 1) and is one of the most important nature conservation areas in southern Australia (Robertson and Armstrong 1999). KI retains almost half of its natural vegetation and is free of feral rabbits and foxes (Robertson and Armstrong 1999). It was also the only region of Australia not inhabited by Aborigines at the time of European colonisation (Lampert 1981; Walshe and Loy 2004). Therefore, KI may retain the best preserved natural ecology in southern Australia. In addition, KI is the only land-bridge island on Earth known to have Late Quaternary vertebrate, vegetative and associated environmental records of significant duration. Black Creek Swamp samples fauna between 110 and 45 kyr ago (Wells *et al*. 2006) and the Seton Rockshelter accumulation (Chapter 2) samples the 11 kyr interval leading up to the isolation of KI 8.9 kyr ago (Hope *et al*. 1977; Lampert 1981; Belperio and Flint 1999; Belperio *et al.* 2002). This research analyses faunal change through time within an assemblage excavated from Kelly Hill Cave (KHC; 5K1) in the Kelly Hill

Caves complex which overlaps in part with the Seton assemblage, but continued to accumulate into the early Holocene to 7 kyr ago.

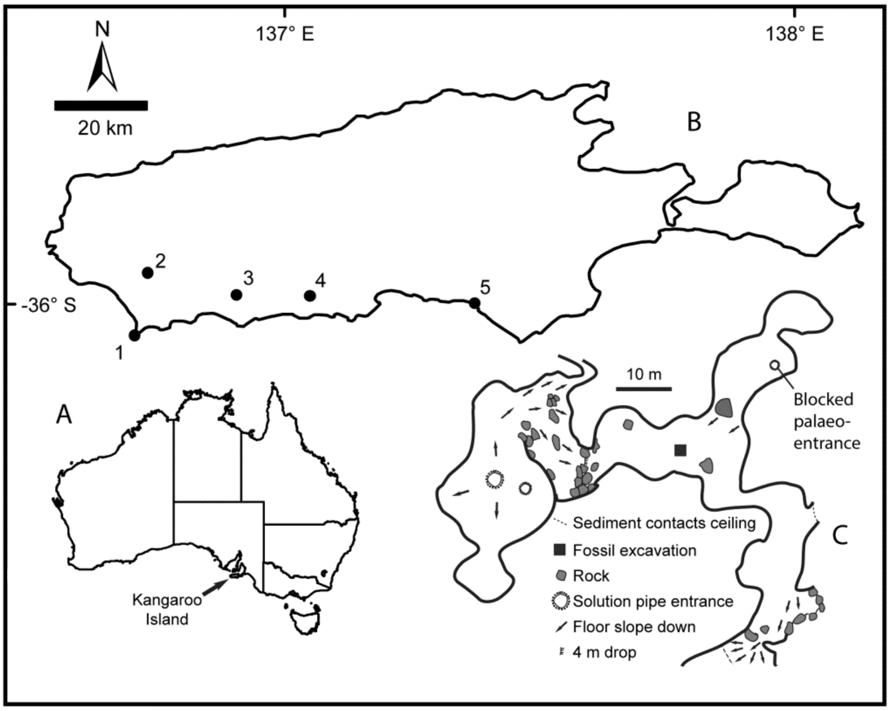


Figure 1A. Location of Kangaroo Island relative to the Australian mainland. B. Location of Late Quaternary fossil assemblages on Kangaroo Island, South Australia. C. Location of the fossil excavation in Kelly Hill Cave (5K1). 1 = Cape Du Couedic Rockshelter. 2 = Black Creek Swamp. 3 = Kelly Hill Cave. 4 = Seton Rockshelter. 5 = Bales Bay.

The vegetation of KI, Fleurieu Peninsula and, southern Eyre and Yorke Peninsulas share striking similarities (Wood 1930; Bickford and Gell 2005) and probably supported similar vertebrate fauna prior to Holocene sea level rise. However, relatively little is known about the origin and evolution of KI's vertebrate fauna. This study aims to establish the composition of KI's Late Pleistocene mammal fauna, and then observe how it has been influenced by climate change and isolation to develop into KI's present day fauna. We then use palaeontological data to test some of the predictions made by MacArthur and Wilson's (1963) theory of island biogeography, which is, to the authors' knowledge, the first time that palaeontological data has been used in this way.

Methods

Chronology

The chronology of the KHC mammal assemblage was reported in Chapter 6 (McDowell *et al*. in review) and is based on AMS radiocarbon and U–Th dating. Radiocarbon ages <11 cal. kyr BP were calibrated using the SHCal04 calibration curve (McCormac *et al*. 2004). Radiocarbon ages >11 cal. kyr BP were calibrated using the IntCal09 calibration curve (Reimer *et al*. 2009). *In situ* speleothems from the surfaces of layers 5, 6, 8, 9 and layer 11 were U–Th dated by multi-collector inductively-coupled plasma mass spectrometry according to the analytical protocols described by Hellstrom (2003).

Palaeontology

The excavation site was selected based on the presence of fossil bones on and in surface sediments, likelihood of stratigraphic integrity, likelihood of minimal disturbance, depth of sediment (determined using a 1.5 m probe) and presence of speleothem growth above the excavation site (suggesting potential speleothem growth in the sediment). A 4-m^2 grid was established to delineate the excavation and was subdivided into 1-m^2 quadrats excavated according to unit using standard paleontological methods. In order to assess stratigraphy, the initial quadrat was excavated in 5-cm spits to a depth of 95 cm. Subsequent excavation was confined to the exposed sedimentary layers, though thicker layers were excavated in 5 cm spits. Layers were then grouped into stratigraphic units. Excavated sediments were sieved and resultant residues were sorted for taxonomically identifiable vertebrate remains (mostly craniodental elements). Nomenclature of recent (extant and historically extinct) mammals follows van Dyck and Strahan (2008). Nomenclature of fossil mammals follows Long *et al*. (2002) with the exceptions that Macropodidae follows

Prideaux and Warburton (2010), Sthenurinae follows Prideaux (2004), Rodentia follows Aplin (2006) and higher systematics follows Wilson and Reeder (2005). The assemblage includes mammal, reptile and amphibian remains. However, due to diagnostic limitations only mammal remains are investigated in detail here. Other taxa will be addressed in future research.

Numbers of identified specimens (NISP) for each species were recorded in a database according to grid, layer and spit, from which NISP for each species within each stratigraphic unit was calculated (Table 1). As a single individual may contribute more than one diagnostic element to the excavated assemblage, NISP values may not be entirely independent. However, as the minimum number of individuals (MNI) is a function of NISP and can generally be relatively accurately predicted from NISP values, “NISP is to be preferred over MNI as the quantitative unit used to measure taxonomic abundance” (Lyman 2008 p. 81). Regardless, the proportional relationship between species should be equivalent irrespective of the abundance measure used. The NISP of each species from each unit was transformed to Relative Abundance ($\mathrm{NISP}_{\mathrm{species}}/\mathrm{NISP}_{\mathrm{total}}$ x 100), the most widely utilized measure of species incidence. Species richness was examined for all species and within different body size classes. Small mammals were defined by body mass <1 kg and large mammals were defined by body mass >1 kg. Species evenness was examined for all species. Variations in fossil samples sizes for different stratigraphic levels or sites greatly influence determinations of species richness (Raup 1975; Barnosky *et al*. 2004, 2005).

Table 1. Relative abundance of non-volant terrestrial mammals excavated from Kelly Hill Cave. RW = reworked unit; * = Species not previously recorded on Kangaroo Island. Indeterminate species identifications were excluded from calculation of richness and evenness.

Units	7	6	5	4	3	2	1c	1b	1a
Layers	15	14	13	12	11	10	9	8-7	6-4
Estimated age (kyr)	45	40	30	20	19	RW	9.5	8	7
Tachyglossus aculeatus	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.15
Antechinus flavipes	1.75	1.69	1.66	0.33	0.10	0.03	0.00	0.00	0.00
Antechinus sp. indet.	0.00	0.00	0.00	0.33	0.00	0.00	0.00	0.00	0.90
Dasyurus maculatus	0.00	0.00	0.00	0.33	0.33	0.30	0.43	0.56	1.05
Dasyurus viverrinus	0.00	0.00	0.13	0.49	0.57	0.61	1.08	1.76	1.35
Dasyurus sp. indet.	0.58	0.00	0.26	0.00	0.10	0.00	0.00	0.00	0.75
Phascogale tapoatafa	0.00	1.69	0.13	0.00	0.00	0.03	0.00	0.00	0.15
Phascogale sp. indet.	0.00	0.00	0.13	0.00	0.00	0.03	0.00	0.00	0.00
Sarcophilus harrisii	0.00	0.00	0.13	0.00	0.03	0.10	0.43	0.19	0.90
Sminthopsis aitkeni	1.75	0.00	0.77	1.14	0.80	2.54	1.29	1.20	1.94
Sminthopsis crassicaudata	0.00	0.00	0.13	0.16	0.33	0.03	0.00	0.09	0.00
Sminthopsis murina	0.00	0.00	0.00	0.00	0.07	0.14	0.00	0.09	0.15
Sminthopsis sp. indet.	1.75	0.00	2.56	3.10	1.13	0.74	0.43	0.65	2.54
Isoodon obesulus	0.00	3.39	0.00	0.00	0.43	0.44	1.72	1.39	2.24
Perameles bougainville	2.34	8.47	1.79	0.98	0.63	0.81	0.00	0.74	1.20
Perameles sp. cf. *P. bougainville*	1.75	0.00	1.15	0.00	0.00	0.00	0.00	0.00	0.00
*Perameles gunnii**	0.00	0.00	0.77	0.33	0.03	0.00	0.00	0.00	0.00
Perameles sp. indet.	0.00	0.00	1.15	0.00	0.00	0.00	0.00	0.00	0.00
*Acrobates pygmaeus**	0.00	0.00	0.00	0.00	0.03	0.10	0.00	0.00	0.45
Cercartetus concinnus	0.00	0.00	0.00	0.33	0.07	0.14	0.00	0.83	3.89
Cercartetus lepidus	0.58	0.00	0.38	0.49	1.26	0.34	0.43	0.37	0.45
*Cercartetus nanus**	0.58	0.00	0.90	0.00	0.00	0.00	0.00	0.00	0.45
Pseudocheirus peregrinus	0.58	0.00	0.51	0.00	0.00	0.00	0.00	0.00	0.00
Trichosurus vulpecula	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.19	0.15
Bettongia lesueur	0.00	0.00	0.26	0.98	0.13	0.00	0.00	0.00	0.00
Bettongia sp. cf. *B. lesueur*	0.00	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.00
Bettongia penicillata	0.00	0.00	0.00	0.49	0.03	0.00	0.22	0.19	0.00
Bettongia sp. indet.	0.00	0.00	0.13	0.00	0.07	0.00	0.22	0.09	0.15
Potorous platyops	0.00	0.00	1.79	2.77	1.36	1.66	1.51	2.87	2.09
*Potorous tridactylus**	2.92	1.69	1.54	0.00	0.03	0.00	0.00	0.00	0.00
Potorous sp. indet.	0.00	0.00	0.26	0.00	0.00	0.00	0.00	0.00	0.00
Phascolarctos cinereus	0.00	0.00	0.26	0.00	0.00	0.00	0.00	0.00	0.00
Lagorchestes leporides	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.19	0.00
Macropus eugenii	0.00	0.00	0.00	0.00	0.00	0.14	3.88	0.65	0.90
Macropus fuliginosus	1.17	0.00	3.33	0.33	0.00	0.27	1.08	0.46	1.79
Macropus sp. cf. *M. fuliginosus*	4.09	5.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Macropus greyi	1.17	0.00	1.79	0.16	0.00	0.03	0.00	0.09	0.00
Macropus rufogriseus	0.00	0.00	2.43	0.82	0.17	0.00	0.00	0.00	0.15
Macropus sp. indet.	8.19	6.78	2.30	0.00	0.13	0.00	0.00	0.19	0.00
*Onychogalea fraenata**	0.00	0.00	0.13	0.00	0.03	0.74	4.09	6.01	4.19
Onychogalea sp. indet.	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.00
*Lagostrophus fasciatus**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.15
‘*Procoptodon*’ *browneorum*	0.58	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
‘*Procoptodon*’ *gilli*	1.75	0.00	2.18	0.65	0.00	0.00	0.00	0.00	0.00
‘*Procoptodon*’ sp. indet.	0.00	0.00	0.13	0.00	0.00	0.00	0.00	0.00	0.00
*Hydromys chrysogaster**	0.00	0.00	0.13	0.00	0.03	0.00	0.00	0.00	0.00
Mastacomys fuscus	0.58	8.47	0.90	2.94	2.43	1.02	0.43	1.85	1.79
*Notomys mitchellii**	0.00	0.00	0.00	0.00	0.83	0.64	0.00	0.28	0.00
*Pseudomys apodemoides**	8.19	8.47	6.91	2.77	0.37	0.10	0.22	0.09	0.15

Table 1cont.

Units	7	6	5	4	3	2	1c	1b	1a
Layers	15	14	13	12	11	10	9	8-7	6-4
Estimated age (kyr)	45	40	30	20	19	RW	9.5	8	7
Pseudomys auritus	0.00	0.00	0.13	0.65	1.80	0.51	0.00	1.39	1.05
Pseudomys australis	0.00	1.69	0.64	9.30	11.61	7.07	7.76	6.48	7.47
*Pseudomys gouldii**	0.00	0.00	0.00	0.16	0.00	0.00	0.00	0.09	0.15
Pseudomys occidentalis	13.45	3.39	7.94	24.80	27.21	28.12	23.06	18.22	17.79
Pseudomys shortridgei	4.09	0.00	0.90	7.67	14.64	20.24	20.69	15.17	11.06
Pseudomys sp. indet.	0.00	0.00	0.77	2.77	3.79	1.25	0.00	0.37	1.05
Rattus fuscipes	31.58	30.51	43.66	31.81	27.15	29.78	30.60	36.54	28.40
Rattus lutreolus	10.53	18.64	7.68	2.94	2.26	1.83	0.43	0.65	2.99
Rattus sp. indet.	0.00	0.00	1.15	0.00	0.00	0.00	0.00	0.00	0.00
Total	100	100	100	100	100	100	100	100	100
Richness	18	12	29	25	29	29	18	28	30
Evenness	0.72	0.80	0.61	0.64	0.57	0.55	0.66	0.62	0.70

Table 2: (opposite) Terrestrial non-volant mammals recorded on Kangaroo Island after isolation by sea-level rise. x = specimen recorded; o= present by inference but no specimen recorded; r = reported present post-settlement but no specimens recorded; * = Re-identified museum specimen (Kemper *et al*. 2010), Cape Du Couedic Rockshelter data after Langeluddecke (2001); Bales Bay data after Walshe (pers. comm.); Present day data after Robinson and Armstrong (1999); Inns (2002).

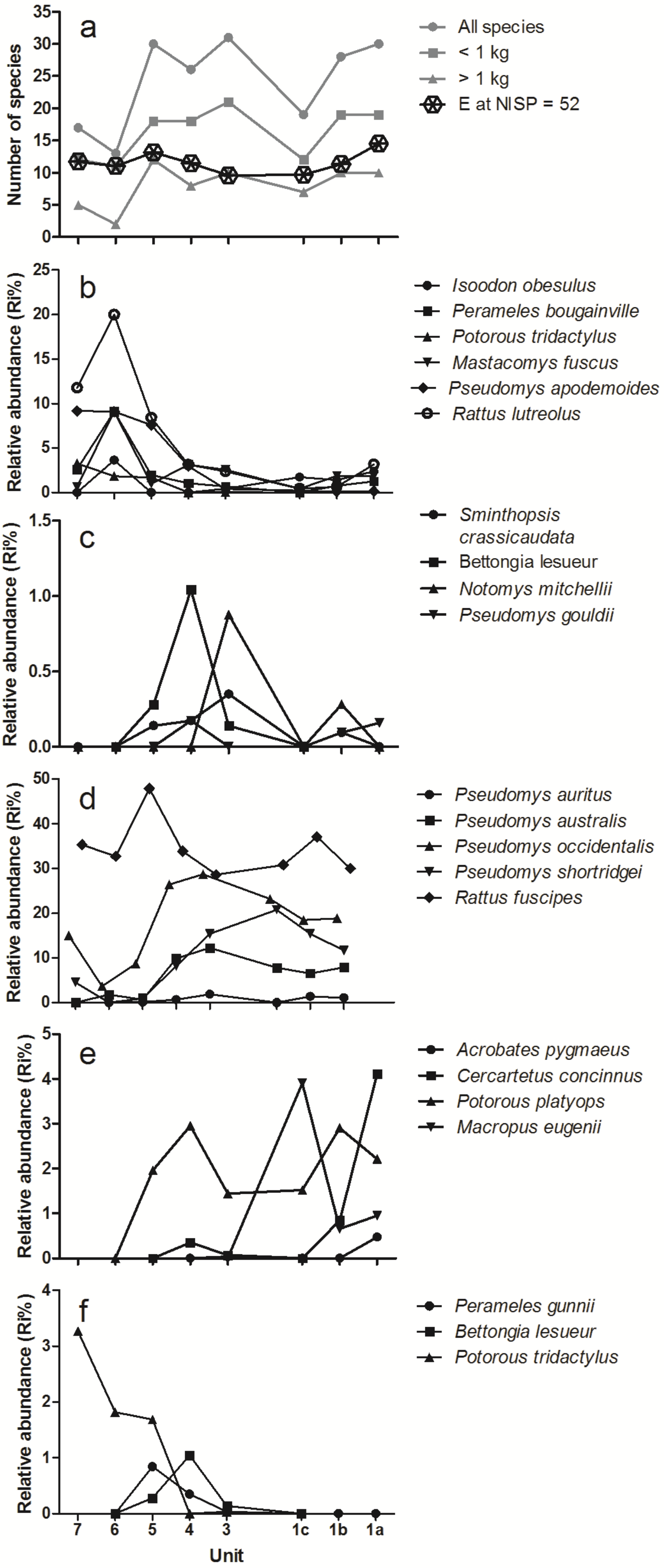
Source	Kelly Hill Cave			Cape Du Couedic Rockshelter				Bales	Present
	Unit 1c	Unit 1b	Unit 1a	L4	L3	L2	L1	Bay	day
Mean age (kyr)	9.5	8	7	?	6.3	?	4.7	0.2	-
Tachyglossus aculeatus	o	o	x	o	o	o	o	x	x
Antechinus sp. indet.	o	o	x						
Dasyurus maculatus	x	x	x	x	x	x	o	x	r
Dasyurus viverrinus	x	x	x						
Phascogale tapoatafa	o	o	x	o	o	o	o	o	r
Sarcophilus harrisii	x	x	x	x	o	o	x		
Sminthopsis aitkeni	x	x	x	o	x	o	o	o	x
Sminthopsis crassicaudata	o	x							
Sminthopsis murina	o	x	x	o	o	o	o	x	
Isoodon obesulus	x	x	x	x	x	x	x	x	x
Perameles bougainville	o	x	x	o	o	o	o	x	
Acrobates pygmaeus	o	o	x	o	o	o	o	x	
Cercartetus concinnus	o	x	x	o	o	o	o	o	x
Cercartetus lepidus	x	x	x	o	o	o	o	o	x
Cercartetus nanus	o	o	x						
Pseudocheirus peregrinus	o	o	o	o	o	o	o	o	x
Trichosurus vulpecula	o	x	x	o	o	o	o	x	x
Bettongia penicillata	x	x							
Potorous platyops	x	x	x	x	x	x	x	x	
Lasiorhinus latifrons	o	o	o	o	x	x	x		
Lagorchestes leporides	o	x							
Macropus eugenii	x	x	x	o	o	o	o	x	x
Macropus fuliginosus	x	x	x	o	o	o	o	x	x
Macropus greyi	o	x							
Macropus rufogriseus	o	o	x						
Onychogalea fraenata	x	x	x						
Lagostrophus fasciatus	o	o	x						
Mastacomys fuscus	x	x	x						
Notomys mitchellii	o	x							
Pseudomys apodemoides	x	x	x						
Pseudomys auritus	o	x	x	x					
Pseudomys australis	x	x	x						
Pseudomys gouldii	o	x	x						
Pseudomys occidentalis	x	x	x	o	o	x	o	x	
Pseudomys shortridgei	x	x	x	x	o	o	o	o	x*
Rattus fuscipes	x	x	x	x	x	x	x	x	x
Rattus lutreolus	x	x	x	o	o	o	o	o	x
Richness	18	28	30	7	6	6	5	10	14
Inferred richness (x+o)	35	35	30	22	21	21	21	19	-
Cumulative % richness lost	-	0.0	14.3	37.1	40.0	40.0	40.0	45.7	60.0

Rarefaction analysis using PAST (ver. 2.17; Hammer *et al*. 2001) was undertaken to examine the influence of sample size differences in mammal species richness values of the KHC sequence using the lowest recorded unit NISP (excluding indeterminate identifications) to standardise the expected species richness from each unit (Fig. 2a). PAST was also used to produce rarefaction curves. The ecological characteristics, distribution and body mass of all recent mammals recorded in the KHC fossil assemblage are summarised in Table S1. These data were used to interpret changes in the ecology and structure of the fossil assemblage that may be attributable to the effects of climate change and/or isolation. A large part of the Holocene fossil record was not recorded by the KHC sequence. Consequently, fauna for the period between 7 kyr ago and present was collated from published KI zooarchaeological records (Table 2). Where a species occurred in a younger assemblage, it was assumed to have occurred on the island since isolation and its presence was therefore inferred when absent from older post-isolation assemblages.

Stable-Isotope Analysis

Variations in stable carbon and oxygen isotopes in land-snail shells reflect the isotopic contents of diet vegetation and ingested waters, as well as temperatures and relative humidity's (Balakrishnan and Yapp 2004). We analysed 43 *Cupedora* spp. shells from the KHC sequence and six modern specimens from the land surface above following the methods described by Prideaux *et al*. (2010). Land-snail shells were treated with 3% H_2O_2 to remove organic compounds, washed in fresh 3% H_2O_2 then washed repeated in distilled water using an ultrasonic bath to remove particulates.

Figure 2: Mammal species richness and relative abundance trends from Kelly Hill Cave, Kangaroo Island. (a) Species richness of all mammals, small mammals (< 1 kg) and large mammals (> 1 kg). Expected species richness (E) is derived from rarefaction analysis (SI appendix). (b) Relative abundance of taxa that decline from the Late Pleistocene into the Holocene (c) Relative abundance of taxa that peak during the LGM (d and e) Relative abundance of taxa that increase from the Late Pleistocene into the Holocene and *Rattus fuscipes* which does not appear to follow any trend (f) Relative abundance of taxa that disappear form the Kelly Hill Cave sequence.



Powdered samples of land-snail shell aragonite (~200 μg) were reacted at 90°C in a Kiel carbonate device and analysed on a Finnigan MAT251 mass spectrometer. Isotope results were standardized to the V-Peedee Belemnite scale by in-run comparison with NBS-19 and NBS-18. $\delta^{13}C$, $\delta^{18}O$ ‰ = [(Rsample/Rstandard) –1] × 1000, where R is the $^{13}C/^{12}C$ or $^{18}O/^{16}O$ ratio. Reproducibility of $\delta^{13}C$ and $\delta^{18}O$ for NBS-19 (n = 11) during the period of analysis was ± 0.02‰ and ± 0.03‰ (both at 1σ), respectively.

Results

Chronology

AMS radiocarbon (Table S3) and U–Th dating (Table S4) of bone and speleothem respectively indicate that unit 1 accumulated when KI was isolated from the mainland. Unit 1a accumulated 7.5–6.6-kyr ago, unit 1b accumulated 9–7.5-kyr ago and unit 1c accumulated 9.8–10.2-kyr ago. Dating results indicate that unit 2 has been reworked and that unit 3 accumulated 20–18-kyr ago during the LGM. Due to poor bone collagen preservation and the absence of speleothem and charcoal, units 4–7 have not yet been dated (McDowell *et al*. in review). *In situ* sthenurine (short-faced) kangaroos occur in unit 7 only. Sthenurine remains from nearby Black Creek Swamp have been dated to ≥45 kyr (Wells *et al*. 2006), tentatively suggesting a minimum age of 45 kyr to be ascribed to unit 7, which in turn suggests that units 6–4 accumulated between 45 and 20 kyr ago.

Stable Isotopes

All $\delta^{13}C$ results fall within the range of pure C_3 plant diet (Fig. 3). Slight differences between Late Pleistocene and Holocene $\delta^{13}C$ values probably indicate minor differences in habitat and dietary preferences (i.e. shaded versus more open; grass versus trees) but may also vary slightly due to variable consumption of local limestone by land snails. However, $\delta^{13}C$ values obtained with radiocarbon ages suggest a stronger relationship (Table S3). Bones aged > ~17 kyr old (Table S3) have $\delta^{13}C$ values of –17.6 to –17.0‰ whereas bones aged 7–10 cal kyr BP have $\delta^{13}C$ values of –23.0 to –21.4‰. These $\delta^{13}C$ values likely reflect a shift from xeric, more open canopy vegetation in the late Pleistocene to more mesic, closed canopy conditions in the early Holocene. Average $\delta^{18}O$ values obtained from recent and unit 1 (Holocene) shells are very similar though Holocene estimates appear to be slightly higher than the present day (Fig. 3). In contrast, average $\delta^{18}O$ values obtained from unit 3 (LGM) are much higher, suggesting that LGM humidity was lower than during the Holocene. However, all other Late Pleistocene $\delta^{18}O$ values obtained are more similar to modern than LGM values (Fig. 3).

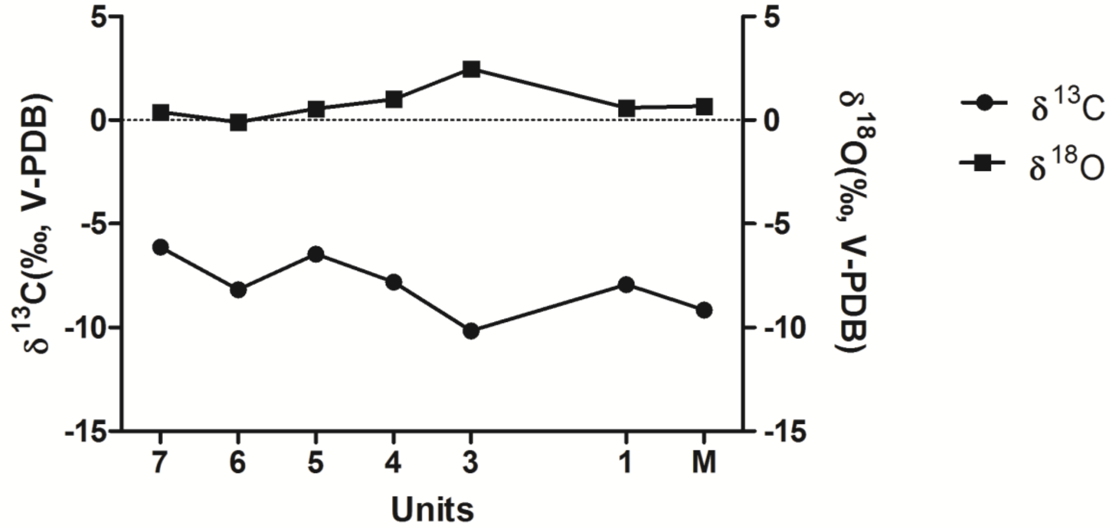


Figure 3: Average $\delta^{13}C$ and $\delta^{18}O$ values from modern (M) and fossil land snail shells excavate from each stratigraphic unit of the Kelly Hill Cave excavation, Kangaroo Island.

Faunal trends through time

All units contain a broad size range of mammals, but species weighing <500 g predominate. Several associated and articulated specimens were discovered and rodent splanchnocrania were common, suggesting minimal reworking (see SI Appendix). Species body mass and the lack of digestive erosion and carnivore tooth marks suggest that the assemblage accumulated by a combination of owl predation and pitfall trapping. Further, the consistent broad size range of species throughout the KHC sequence (Table 1; TableS2; SI Appendix) implies that the accumulation mechanisms were consistent through time. Therefore, changes in species relative abundances between units are likely to accurately reflect changes in the community prompted by environmental changes (Prideaux *et al*. 2007, 2010) or in this case potentially the effects of isolation.

Of the 43 mammals recorded in this study, 10 are new to KI (Table 1). Most newly recorded species were rare, but *Pseudomys apodemoides* was present in every excavation unit suggesting that it was an important member of the KI mammal palaeocommunity. Species richness (Table 1) was highest in unit 1a (30 species), closely followed by unit 5 (29 species) and was lowest in unit 6 (13 species), indicating a relationship between unit thickness/sample size and mammal diversity (Fig. 4). Rarefaction, which corrects for sample size, shows that mammal richness (Fig. 2a) and evenness (Table 1) was fundamentally stable through time and rarefaction curves (Fig. S2) approach asymptote in all units except unit 6, indicating that it is unlikely additional specimens would yield many additional species.

Heath-dwelling species were abundant in unit 7 (~45 kyr ago; Fig. 2b), declined in units 6–4 (45–20 kyr ago) and were rare in units 3 and 1 (20–7 kyr ago). In contrast, a number of mallee woodland (Fig. 2d) and woodland–forest (Fig. 2e) species were either absent or rare in units 7–5, began to increase in abundance in unit 4, remaining relatively abundant for the remainder of the record, suggesting more mesic conditions. The relative abundance of arid and semi-arid species peaked in units 4 and 3 (Fig. 2c), the latter at least accumulating during the LGM. *Rattus fuscipes* maintained consistently high relative abundances in all units (Fig. 2d). Two species of sthenurine (*'Procoptodon' gilli, 'P.' browneorum*) were recovered from unit 7, with remains of *'P.' gilli* clearly *in situ* by virtue of preservation and close association (SI picture). Isolated teeth were found in units 4 and 5 but are absent from units 3–1.Three species of mammal (*Perameles gunnii*, *Bettongia lesueur*, *Potorous tridactylus*) disappear from the KHC sequence in unit 3, 20–18 kyr ago (Fig. 2f). Their disappearance correlates with the LGM, which might imply that they coped poorly with a relatively arid climatic extreme. However, each species is rare in units 7–4, and *B. lesueur* is an arid-zone specialist (Claridge *et al*. 2007) and was present in the Seton Rockshelter assemblage until about 10 kyr ago so the disappearance of these mammals from the KHC assemblage during the LGM may simply result from stochasticity. Five species (*Sminthopsis crassicaudata*, *B. penicillata*, *Lagorchestes leporides*, *Macropus greyi*, *Notomys mitchellii*) disappeared from the KHC sequence after sea-level rise isolated KI from the mainland, but again, these species are comparatively rare throughout the fossil sequence.

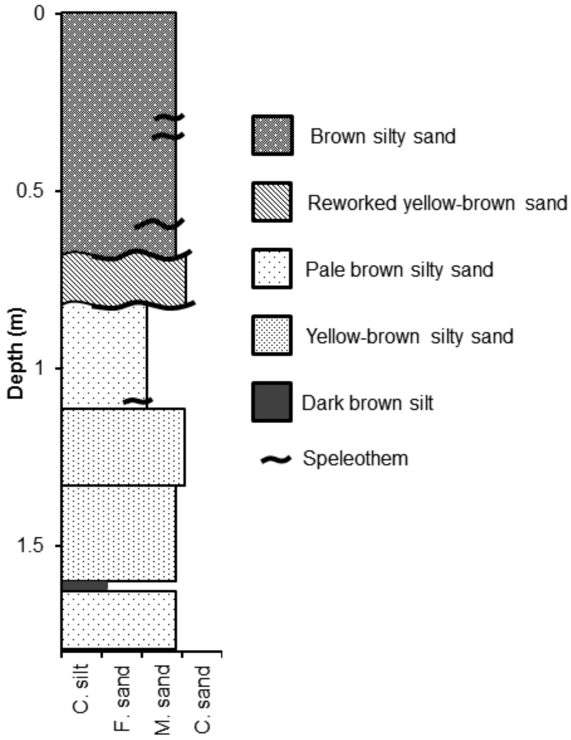


Fig. 4: Stratigraphic profile of the Kelly Hill Cave excavation indicating unit thickness, general composition, grain size and location of dated speleothems.

Holocene zooarchaeological records from Cape Du Couedic Rockshelter (Langeluddecke 2001) and Bales Bay (Walshe pers. comm.), along with the post-European occurrences (Robinson and Armstrong 1999; Inns 2002), were used to further investigate species loss from the KI mammalian fauna. Table 2 shows that richness decreased by 14.3% between unit 1b and unit 1a of the KHC excavation and that an additional 23% of richness was lost between unit 1a of the KHC excavation and the oldest level in the Cape Du Couedic Rockshelter assemblage. Several small macropodids and rodents appear to have been lost during the intervening period though this may be a consequence of changing taphonomic bias. Species richness then remained stable in the Cape Du Couedic assemblage until its accumulation ceased 4.7 kyr ago. The Bales Bay assemblage accumulated about 200 years ago

(Walshe pers. comm.) and includes all of the species found at Cape Du Couedic except *Sarcophilus harrisii* and *Lasiorhinus latifrons,* the loss of which represents an additional 9% decrease in richness. Given that the Bales Bay assemblage was accumulated by European fur traders (Walshe pers. comm.), the absence of these two relatively large mammals probably reflects true absence from the island. Only 13 mammals were recorded by Europeans after official settlement in 1836, highlighting a further 26% loss of richness compared with the Bales Bay assemblage. Overall, 60% of KI's mammal richness has been lost since it was isolated by rising Holocene sea-levels.

Discussion

Effects of climate change

Gingele *et al*. (2007) reconstructed late Quaternary palaeoclimatic change in southeastern Australia using multiple climate proxies from a deep-sea core collected south of southwestern KI. Between 17 and 13.5 kyr ago fluvial clays derived from the combined Murray and Darling River catchment dominated the core sediments, indicating strong deglaciation outflow from the Murray-Darling Basin. From 13.5 kyr ago to present sediments began to change from fluvial to aeolian deposition, indicating a trend towards more arid conditions and strengthening westerly winds on the adjacent mainland during the Holocene. This trend was punctuated by 2 periods of fluvial sedimentation derived from the Murray catchment between 13.5–11.5 kyr ago and 9.5–7.5 kyr ago, indicating more humid conditions in the southern part of the Murray-Darling Basin. Aeolian dust deposition increased between 7.5–5 kyr ago then persisted until the present, but peaking about 1.5 kyr ago. This record compares well with palaeoclimatic interpretations of Lake Keilambete (Bowler 1981; De Deckker 1982; Chivas *et al*. 1993) and Blue Lake (Stanley and De Deckker 2002).

Palynological records from southeastern Australia have been extensively investigated (Dodson 1974, 1975, 1977, 2001; Dodson & Wilson 1975; D'Costa *et al*. 1989; Edeny *et al*. 1990; D'Costa & Kershaw 1995; Harle 1997; Harle *et al*. 1999; Kershaw *et al.* 1991; Bickford and Gell 2005; Cook 2009). These studies generally agree that about 50 kyr ago, the vegetation of southeastern Australia changed from *Eucalyptus* forest with heath understorey to *Eucalyptus* woodland with heath and grass understorey or open grassland-steppe. 25–12 kyr ago woodlands become more open with *Casuarina* and *Banksia* species becoming more prominent. Between 12 kyr and the present, closed *Casuarina*/*Eucalyptus* woodlands predominated. These vegetation changes reflect the overall trend that south-eastern Australia experienced a drier and more seasonal climate during the Quaternary (Kershaw, 1995; Kershaw *et al*. 1991).

Pollen records from KI are limited to Lashmar Lagoon (Clark 1976; Clark and Lampert 1981; Singh *et al.* 1981) which spans the last 10 kyr and Black Creek Swamp, Flinders Chase which is thought to have a minimum age of approximately 19 kyr (G. Hope *et al.* 1977; Forbes *et al*. 2004; Wells *et al*. 2006). Lashmar Lagoon's pollen sequence suggests that about 7 to 6.4 kyr ago KI's vegetation was more open than at any subsequent time before European colonisation. During this period *Casuarina* spp. increased in abundance while Chenopod heath and grasses dominated the understorey and probably covered large open areas. *Casuarina* woodlands persisted from about 6.4 to 4.8 kyr indicating a wetter climate than today (Clark and Lampert 1981). However, around 4.8 kyr *Casuarina* spp. were replaced by more arid tolerant *Eucalyptus* spp. Woody shrubs increased at the expense of grasses and persisted from 4.8 to 1.3 kyr ago. The pre-European vegetation of KI was predominantly open Eucalyptus woodland on the lateritic plateau and open mallee scrub on Pleistocene calcarenite (Singh *et al*. 1981). Pollen from Black Creek Swamp indicates change from grassland to wet shrubland to drier Eucalypt trees then back to a wet swamp, and suggests unusually wet conditions during the LGM. Faunal change through the KHC sequence appears to correlate with environmental change identified by Gingele *et al*. (2007) and mainland pollen records. However, both Holocene aged fauna and sediments (chapter 6) suggest that KI experienced more mesic conditions than those interpreted by Gingele *et al*. (2007) for southeastern Australia.

Faunal trends in the KHC assemblage reveal that species adapted to dry heath were most abundant in pre-LGM units and diminished during the LGM, but still persisted in low abundance into the Holocene. In contrast, woodland species were relatively rare in Late Pleistocene units but became much more abundant in Holocene units. These shifts correlate with an increase in canopy cover indicated by $\delta^{13}C$ values and suggest a decrease in heath and grassland. Even though relative abundances changed dramatically during the LGM, only three mammal species (*P. gunnii*, *B. lesueur* and *P. tridactylus*) disappeared from the sequence at that time, bolstering the view that southern Australia's mammals were highly resilient to climate change (Prideaux *et al*. 2007, 2010; Macken *et al.* 2012).

Interestingly, the relative abundances of more mesic-adapted species increased before Holocene conditions came into full effect. This may be due to the proximity of southwestern KI to the continental-shelf, and hence the palaeocoastline, which was less than 50 km south of KI even during the LGM (Lampert 1981; Forbes *et al*. 2009). Combined with semi-continuous Southern Hemisphere westerlies (Shulmeister *et al*. 2004; De Deckker *et al*. 2012), southwestern KI probably experienced ameliorating maritime conditions and greater precipitation at a time when most parts of southern Australia experienced peak aridity (Gingele *et al*. 2007).

Stable-isotope analyses of land snail shells from KHC indicate a diet of predominantly C_3 vegetation (Fig. 3) which is consistent with the modern vegetation. Forbes *et al*. (2009, 2010) analysed organic matter sampled from Black Creek Swamp that accumulated between 31–18 kyr ago and made similar findings. However, Gröcke and Bocherens (1996) suggested that the diet of some fossil species sampled from Black Creek Swamp consisted of C_4 plants. Given that the Black Creek Swamp assemblage is composed of three differently aged layers, Gröcke and Bocherens' (1996) findings may relate to differences in the age of the fossils studied.

The similarity between modern and Late Pleistocene oxygen isotopes results are difficult to interpret. Factors determining land-snail shell oxygen isotopes can be quite complicated, but empirical studies of modern land snails have shown $\delta^{18}O$ values of shell aragonite to be related to rainfall or relative humidity (Yapp 1979; Margaritz *et al*. 1981; Goodfriend *et al*. 1989; Balakrishnan *et al*. 2005). Based on faunal guilds we infer more arid conditions in the Late Pleistocene. Under lower humidity conditions, land snail diets should be enriched in ^{18}O but with the exception of results obtained from LGM aged land snail shells, elevated Late Plistocene $\delta^{18}O$ values were not observed. Forbes *et al*. (2010) obtained similar results from isotopic analysis of fossil tooth enamel from Black Creek Swamp. Anomalous $\delta^{18}O$ values could be caused by diagenesis, which correlates with poor bone collagen preservation in units 4–7 (see Chapter 6) but should result in recrystallization of shell aragonite (Prideaux *et al*. 2010). Forbes *et al*. (2010) proposed that a simultaneous decrease in temperature and relative humidity may result in equivalent modern and fossil δ^{18}O values, a hypothesis that is consistent with previous palaeoclimate studies that have inferred cooler and drier conditions during the Late Pleistocene (Wells et al. 2006; Forbes *et al*. 2009).

Seton Rockshelter (Chapter 2), an archaeological site, is the only assemblage on KI that overlaps temporally with the KHC assemblage. Small quantities of stone tools occur in several of the deeper subunits (Hope *et al*. 1977; Lampert 1981) indicating periodic short term use by humans. However, the quantity of stone tools increases dramatically around 17 kyr ago, suggesting an increase in the frequency or intensity of human occupation. The Seton assemblage contains similar fauna to the KHC assemblage but does not adhere to the same faunal trends. In the pre-LGM strata of both the Seton and KHC sequences heath species were highly abundant. However, in the Seton assemblage heath species remained highly abundant until human activity (as indicated by stone tool quantity) intensified, at which point their abundance dropped dramatically. Conversely, forest/woodland species were relatively less abundant throughout the Seton sequence until human activity intensified, after which their abundance increased dramatically. In addition, the relative abundance of many rodent species which were most likely accumulated by owls plummeted when human occupation intensified. These faunal changes are attributed to a change in the mode of accumulation from primarily *S. harrisii* and owls in subunits l–f to primarily humans in subunits e–b. In contrast, the entire KHC assemblage is attributed to a combination of owl predation and pitfall trapping. Changes in species relative abundance are thought to represent changes in environment resulting from either changing climate or degree of isolation. Hope *et al*. (1977) suggested that faunal change in the Seton assemblage was driven by climate change. However, the intensification of human occupation and climate change appear to be contemporaneous making it impossible to determine the cause of faunal change. It is entirely possible that human occupation of Seton Rockshelter intensified in response to increasing availability of surface water at the site due to increasing relative humidity associated with post LGM conditions. Differences in the modes of accumulation of the Seton and KHC assemblages probably account for differences in faunal trends observed in the two sites.

Island biogeography and the effects of isolation

Island biogeography theory predicts that diverse ‘mainland’ faunas isolated by sea level rise will suffer elevated selection pressures that result in an asymmetric extinction rate. After rising Holocene sea levels isolated KI about 8.9 kyr ago (Belperio and Flint 1999), mammals began to disappear from the palaeontological and zooarchaeological record (Table 3). Between 9.5 and 8 kyr ago the inferred species richness if KI did not change. However, between 8 and 7 kyr ago 14% of KI’s fauna disappeared from the fossil record and between 7 and 6.3 kyr ago a further 25% of KI’s fauna was lost. Between 6.3 and 4.7 kyr ago the inferred mammal richness of KI was stable and between 4.7 and 0.2 kyr ago less than 6% of KI’s fauna disappeared. However, between 0.2 kyr ago and present a further 14% of the KI’s fauna was lost, leaving the Island with 40% of its pre-isolation Holocene fauna. The combined fossil record demonstrates that KI’s non-volant Holocene mammal fauna experienced an initial period of rapid extirpation soon after isolation, followed by a period of relative stability, which supports island biogeography theory’s prediction of an asymmetric extinction rate. Therefore, isolation appears to have had a much greater impact on the non-volant mammals of KI than the effects of climate change.

Island biogeography theory also predicts that species with higher resource requirements such as predators and large herbivores should be among the first to be extirpated. KI's fossil record appears to support this prediction for carnivores, but not herbivores. *D. maculatus* persisted on KI up until European colonisation and *S. harrisii* persisted until at least 4.7 kyr ago, whereas *D. viverrinus* was last recorded some 7 kyr ago (Table 2).

There are no data for the energy requirements of *D. maculatus*, but *S. harrisii* has a mean apparent energy intake of 469 kJ/kg compared with 776 kJ/kg for *D. viverrinus* (Green and Eberhard 1979). In Tasmania, competition between *S. harrisii*, *D. maculatus*, and *D. viverrinus* is mitigated by niche differentiation (Jones and Barmuta 1998, 2000) *D. maculatus* avoids direct competition with *S. harrisii* by hunting arboreal prey and *D. viverrinus* avoids direct competition with *S. harrisii* and *D. maculatus* by using grassland more than the other species and hunting invertebrates (Jones and Barmuta 1998). If similar niche differentiation occurred on KI, *D. maculatus* would have a broader niche than *D. viverrinus* which might be further disadvantaged by the rarity of grassland on KI during the Holocene.

There are no data for the energy requirements of *Lagorchestes leporides, Macropus fuliginosus, Macropus greyi, Macropus rufogriseus, Onychogalea fraenata* or *Lagostrophus fasciatus* but *M. giganteus* (assumed to be equivalent to *M. fuliginosus*) requires 570 kJ/kg, *M. eugenii* 320 kJ/kg (Dellow and Hume 1982), *L. latifrons* requires 140 kJ/kg (Barboza *et al*. 1993) and *T. vulpecula* requires 370 kJ/kg (Harris *et al*. 1985). *L. latifrons* clearly has a much lower energy budget than the kangaroos and possum that still occur on KI today but may also have been disadvantaged by the rarity of grasslands on KI during the Holocene.

Table 3: Native non-volant mammal faunas of Kangaroo Island, Murray Mallee, Eyre, Yorke and FluerieuPeninsulas, South Australia. Eyre Peninsula is divided into a southwestern zone (south and west of the 400 mm mean annual rainfall isohyet, Schwerdtfeger, 1985), comparable in area and rainfall range with Yorke Peninsula, and a northern and eastern zone of lower rainfall. Historic Kangaroo Island mammal records from Robinson and Armstrong (1999). Late-Holocene and historic Fleurieu Peninsula mammal records from Armstrong *et al*. (2003) and fauna excavated from Kongarati and Smugglers Caves (unpublished data). Late-Holocene and historic Yorke Peninsula mammal records from McDowell *et al*. (2012) and Neagle (2008). Late-Holocene and historic Murray Mallee mammal records from Wakefield (1966a, b), Lundelius (1983), Foulkes and Gillen (2000) and Robinson *et al*. (2000). Late-Holocene and historic Eyre Peninsula mammal records from Watts and Ling (1985) and Baynes (1987) with modifications, McNamara (1997), McDowell and Medlin (2010) (southwestern zone only) and Kemper *et al*. (2010).

f = fossil record; m = modern record; h = historical record with no specimen; ? = less certain record; - = not recorded.

Species	Kangaroo Island	Murray Mallee	Fleurieu Peninsula	Yorke Peninsula	SW Eyre Peninsula	NE Eyre Peninsula
Tachyglossus aculeatus	m, f	m	m	m	m	m
Antechinus flavipes	f	f	m	-	-	-
Antechinomys laniger	-	-	-	-	-	m, f
Dasycercus sp. indet.	-	f	-	-	f	-
Dasyurus geoffroii	-	h?, f	-	f	f	?
Dasyurus maculatus	m, f	m	-	-	-	-
Dasyurus viverrinus	f	h	m, f	-	-	-
Ningaui yvonneae	-	m	-	-	-	m, f
Parantechinus apicalis	-	-	-	-	f	-
Phascogale calura	-	-	-	f	-	f
Phascogale tapoatafa	m, f	h, f	m	-	?	-
Sarcophilus harrisii	f	f	-	-	-	-
Sminthopsis aitkeni	m, f	-	-	-	-	-
Sminthopsis crassicaudata	f	m	m	f	-	f
Sminthopsis dolichura	-	-	-	m, f	f	m
Sminthopsis griseoventer	-	-	-	f	f	m
Sminthopsis macroura	-	-	-	-	-	m
Sminthopsis murina	h, f	m	m			
Sminthopsis psammophila	-	-	-	-	-	m, f
Thylacinus cynocephalus	-	f	-	-	-	-
Isoodon obesulus	m, f	f	m, f	f	f	-
Perameles bougainville	h, f	m, f	-	f	f	f
Macrotis lagotis	-	m	m	f	f	?
Acrobates pygmaeus	h, f	-	m	-	-	-
Cercartetus concinnus	m, f	m	m	m, f	f	?, f
Cercartetus lepidus	m, f	m	-	-	-	-
Cercartetus nanus	f	m	-	-	-	-
Pseudocheirus peregrinus	h, f	m	m	f	f	-
Trichosurus vulpecula	m, f	m, f	m, f	m, f	f	m
Bettongia lesueur	-	h, f	m	f	f	f
Bettongia penicillata	f	h, f	m	f	f	?, f

Table 3 cont.

Species	Kangaroo Island	Murray Mallee	Fleurieu Peninsula	Yorke Peninsula	SW Eyre Peninsula	NE Eyre Peninsula
Potorous platyops	h, f	f	-	f	f	f
Lasiorhinus latifrons	f	m, f	-	m	m, f	m
Table 3 cont.						
Lagorchestes leporides	f	h, f	-	f	-	-
Macropus eugenii	m, f	m, f	m	f	f	?
Macropus fuliginosus	m, f	m, f	m, f	m, f	m, f	m
Macropus greyi	f	h, f	-	-	-	-
Macropus robustus	-	m	m	m, f	-	m
Macropus rufus	-	m	-	-	-	m
Macropus rufogriseus	f	-	-	-	-	-
Onychogalea fraenata	f	h?	-	-	-	-
Onychogalea lunata	-	f	-	-	-	-
Petrogale xanthopus	-	-	-	-	-	m
Lagostrophus fasciatus	f	f	-	f	-	f
Hydromys chrysogaster	-	f	m	-	-	-
Leporillus apicalis	-	f	-	f	-	f
Mastacomys fuscus	f	f	-	-	-	-
Notomys mitchellii	f	m, f	-	f	f	m, f
Pseudomys apodemoides	f	m, f	f	-	-	-
Pseudomys auritus	f	f	-	-	-	-
Pseudomys australis	f	h?	f	f	f	f
Pseudomys bolami	-	f	-	-	f	f
Pseudomys gouldii	f	m, f	-	f	f	f
Pseudomys occidentalis	h, f	-	-	f	f	f
Pseudomys shortridgei	m, f	-	f	f	f	f
Rattus fuscipes	m, f	m	m	f	m, f	f
Rattus lutreolus	m, f	m, f	m	-	-	-
Rattus tunneyi	-	-	-	f	f	-
Canis lupus	-	m, f	-	f	f	m
Total species	37	44	23	30	28	33+
Number species shared with KI	-	33	19	20	18	15
Percent species shared with KI	-	89.1	51.4	54.1	48.6	40.5

Larger body size engenders ecological advantages such as greater energy efficiency, greater mobility and more efficient homeostatic mechanisms which allow large-bodied species to use a greater range of habitats and dominate resource use within those habitats. Consequently, more individuals of a larger species may be supported on the same amount of energy than a smaller species (Brown and Maurer 1986; Jones and Barmuta 1998). In addition, competitive and numerical dominance in interspecific interactions may favour larger species. Island biogeography theory does not take into account life history factors, interspecific interference, anthropogenic environmental modification or selective hunting (Laurance 2008). These factors may affect species differentially, which may explain why this prediction appears valid for some species but not others.

Regional biogeography

Many of the non-volant mammals found on KI also once occurred on adjacent mainland areas (Table 3). As expected, faunal similarities decrease as distance between the regions increased. Thirteen species were ubiquitous to all regions investigated. KI and northeastern Eyre Peninsula shared 15 species (40.5% of KI's fauna). KI and southwestern Eyre Peninsula shared 18 species (48.6% of KI's fauna). KI and Yorke Peninsula shared 20 species (54.1% of KI's fauna) and KI and Fleurieu Peninsula shared 19 species (51.4% of KI's fauna). Due to the rarity of Holocene fossil assemblages on Fleurieu Peninsula the number of species shared by KI and Fleurieu Peninsula is probably underestimated. Surprisingly, the Holocene mammal fauna of KI was actually most similar to South Australia's Murray Mallee region, with which it shared 33 species (89.1% of KI's fauna). Opperman (1999) reported similarities between Murray Mallee and Fleurieu Peninsula's vegetation, futher suggesting that faunal similarities between KI and Fleurieu Peninsula are underestimated.

Prior to Holocene sea-level rise, mammal populations appear to have been continuous between Eyre and Yorke Peninsulas and the intervening lower-lying area that is now Spencer Gulf (McDowell *et al*. 2012). Therefore, it was expected that many of the mammal species found on KI would have mingled with those of the Eyre, Yorke and Fleurieu Peninsulas in a similar manner. This assumption may be valid, but it appears that the majority of KI's fauna has been derived from South Australia's Murray Mallee bioregion. During the LGM the Palaeo-River Murray ran out over the Lacepede Shelf and flowed almost parallel with and within 50 km of much of the southern coast of KI (Fig. 5; Gingele *et al*. 2004; Hill *et al*. 2009; Schmidt *et al*. 2010).

Mammals living in the Murray Mallee during the late Pleistocene and Holocene appear to have followed the Palaeo-River Murray out onto the shelf and then onto KI. Following Holocene sea-level rise Eyre and Yorke Peninsulas formed virtual islands for terrestrial mammals, bounded by the Southern Ocean to the south and aridity to the north. Late Holocene mammal assemblages from these Peninsulas are comparable in species composition and richness (McDowell and Medlin 2010; McDowell *et al*. 2012) but lack some of the more mesic-adapted species that occur on KI, namely *D. maculatus, D. viverrinus, Acrobates pygmaeus, Cercartetus lepidus, Mastacomys fuscus, P. apodemoides* and *Rattus lutreolus*.

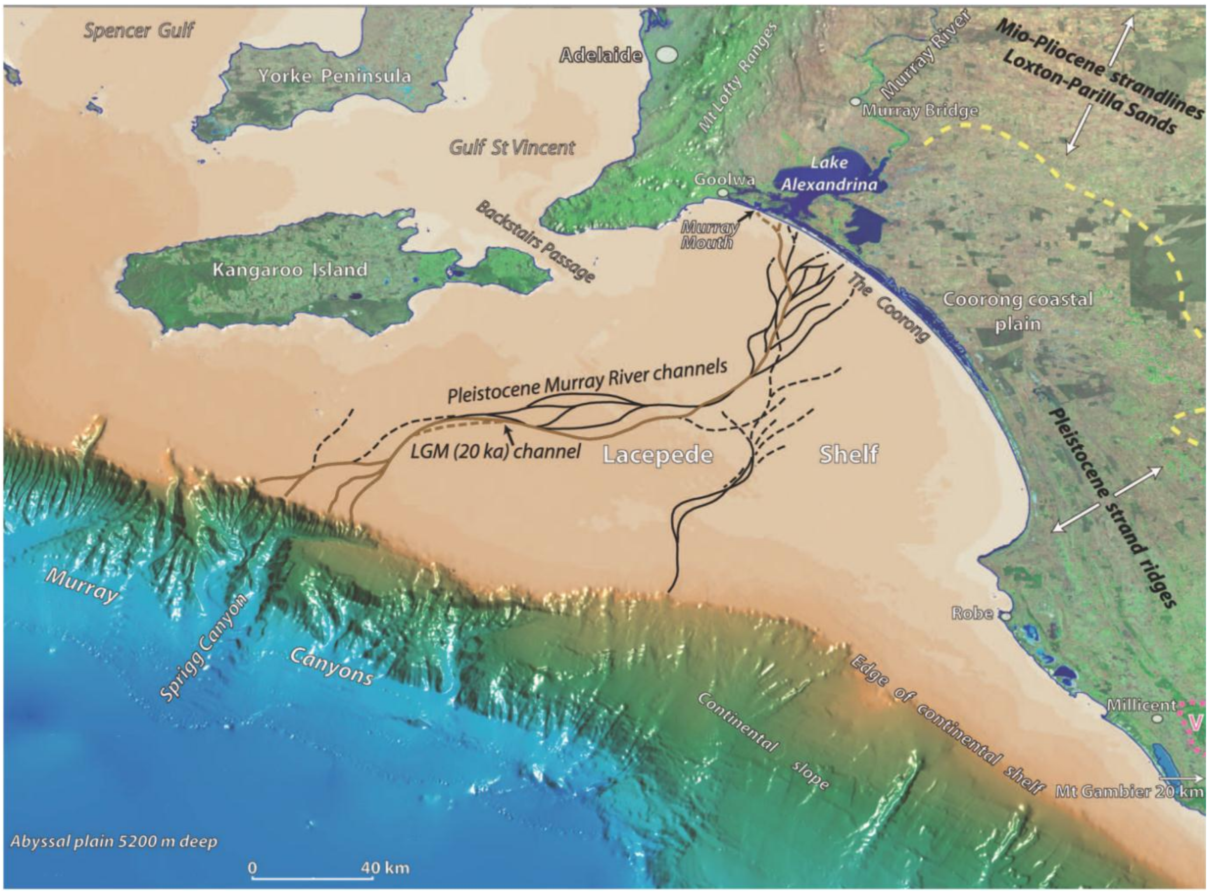


Figure 5: Location of Murray River palaeo-channels (with Last Glacial Maximum channel in brown) on the Lacepede Shelf which flowed southward from the present Lakes Alexandrina and Albert, then roughly west-southwest and into the head of Sprigg Canyon (after Hill *et al*. 2009)

Instead they include more xeric-adapted equivalent species such as *D. geoffroii*, *Dasycercus* sp. indet., *Parantechinus apicalis*, *Phascogale calura*, *Sminthopsis psammophila*, *Leporillus apicalis* and *Pseudomys bolami*. Many of the taxa encountered on KI but absent from Eyre and Yorke Peninsulas have been recorded from Fleurieu Peninsula (e. g., *D. viverrinus*, *P. tapoatafa*, *B. penicillata*, *A. pygmaeus* and *R. lutreolus*; Armstrong *et al*. 2003) and Murray Mallee Bioregion (e. g., *P. apodemoides*, *C. lepidus*; Foulkes and Gillen 2000). This may relate to the higher precipitation experienced by KI and Fleurieu Peninsula, and moisture availability form the River Murray in the Murray Mallee region, but may also relate to KI’s geographic position which makes it easily accessible from any of the surrounding mainland bioregions, including Eyre, Yorke and Fleurieu Peninsulas, the Murray Mallee and the Coorong.

Effects of European colonisation

During the 4.5 kyrs that expired between the accumulation of Cape du Couedic Rockshelter’s youngest layer and the Bales Bay assemblage, less than 6% of KI’s Holocene mammal fauna was lost (Table 3). However, in the following 200 years of European occupation a further 14 % of KI’s fauna was extirpated (Table 3) leaving KI with 40% of its pre-isolation Holocene fauna. European colonisation is almost always associated with accelerated extirpation rates and in KI’s case probably relates to vegetation clearance, the introduction of feral cats and pigs and hunting of specific species for their fur. However, compared with the surrounding mainland bioregions e. g., Eyre Peninsula (McDowell and Medlin 2010) and Yorke Peninsula (McDowell *et al*. 2012), the Holocene fauna of KI has fared quite well. This is probably attributable to the absence of foxes and rabbits and KI’s nutrient deficient soils which has resulted in the retention of a large proportion of native vegetation.

Conservation implications

The occurrence of *P. occidentalis* on KI, Eyre and particularly Yorke Peninsula where the species was still being predated by owls when Europeans colonised (McDowell *et al.* 2012), dispels the assertion that many native species were “shrinking in range prior to the arrival of European man” (Watts and Aslin 1981: 205). Morris (2000) noted that while *P. occidentalis* was not considered threatened in Western Australia, it should still be monitored for further decline because of the extensive post-European range reduction it has experienced. Evidence presented here indicates just how large that range reduction has been.

The fossil record investigated here shows that KI has great potential for the successful re-establishment of threatened native species. It retains suitable habitat for a variety of species and it lacks foxes and rabbits, the control of which makes up a large part of the costs associated with mainland translocations. Unfortunately KI has a large feral cat (*Felis catus*) population (Robinson and Armstrong 1999). Burbidge and Manly (2002) demonstrate an association between the presence of cats and the extinction of native mammal on Australian islands, but in the absence of foxes, cats have been shown to consume significantly more carrion (Molsher 1999; Glen and Dickman 2005) which may slightly alleviate predation pressure. The impacts of cat predation *may* be controllable by reintroducing large native predators. The re-establishment of Gray Wolves in Yellowstone National Park (USA) has demonstrated that the reintroduction of apex predators can control mesopredators and restructure native mammal communities to resemble pre-European death assemblages (Smith *et al*. 2003; Miller 2011). In Australia dingos are known to kill cats and foxes (Paltridge 2002; Allen and Fleming 2012) and Hayward (2009) suggested that Tasmanian devils and Quolls could be reintroduction to mainland Australia to act as mesopredator suppressors.

D. maculatus (Spotted-tailed quoll) and *S. harrisii* (Tasmanian devil) occured in KI's late Holocene fossil record and Europeans reported what is thought to have been Spotted-tailed quolls but did not collect specimens. The species has also been found in a European archaeological assemblage at Bales Bay (Walshe pers. comm.). This species was clearly a part of KI's immediately pre-European mammal community and its reintroduction is easily justified. However, the prey species of Spotted-tailed quolls and feral cats overlap significantly and both exploit arboreal prey (Belcher

1995; Jones *et al*. 2001). Both cats and Spotted-tailed quolls have been recorded killing young of the other species (Burnett 2000) and *D. maculatus* has been recorded killing a large male cat (Troughton 1943). In addition, the two species coexist in Tasmania indicating potential for cohabitation.

Tasmanian devils were extant on KI until at least 4.7 kyr ago. Justifying its reintroduction to KI is more difficult, but given the impacts that Tasmanian Devil Facial Tumour Disease is having on the species (e. g., Jones *et al*. 2007), all efforts should be made to protect the species. Establishing an uninfected population of Tasmanian devils on KI would provide insurance against extinction and may even be used to repopulate Tasmania once Tasmanian Devil Facial Tumour Disease has been controlled. Cat population densities have increased in areas where devils have suffered long term infection, providing circumstantial evidence that devils suppress cat numbers (Coupland and Anthony 2007; Jones *et al*. 2012). If the reintroduction of native predators can suppress feral cats, a number of small native mammals that occur in the fossil record could be re-established on KI, though issues surrounding genetic source material would have to be overcome.

Conclusions

The ecological structure of the KHC fossil assemblage changed dramatically over the last 45 kyr. These changes correlate with known climatic change but suggest that KI experienced more maritime conditions during the LGM than expected across southern Australia. Two sthenurine kangaroo species disappeared from a unit estimated to be at least 45 kyr old, a time when climatic conditions were relatively stable. A further three species disappeared during the LGM when KI was connected to the mainland. Despite dramatic changes in relative abundances during the transition from Late Pleistocene to Holocene conditions, it appears that the majority of KI’s mammal species were quite resilient to climate change and resisted community disassembly well into the Holocene. However, isolation appears to have had a much greater effect on the mammals of KI. The asymmetric pattern of species loss appears to conform to predictions made by the equilibrium theory of island biogeography. However, the prediction that the most resource-demanding species should disappear first appears to be supported for carnivores but not herbivores. This may be due to KI’s relatively large size and the apparent maritime influences that occurred during the LGM or may have been influenced by niche partitioning (e.g. Jones 1997). Post-isolation species loss gleaned from archaeological assemblages that were likely subjected to inherently different biases compared with owl and pitfall accumulations. Therefore, mid and late Holocene owl and pitfall assemblages must be investigated to confirm the pattern observed. This study is the first to directly investigate the nature of species loss from a post-isolation land-bridge island using palaeontological data. Our results confirm that palaeontological data can provide enormous insight into the evolution of community composition. Further, it suggests that few reserves are of adequate size to conserve fauna in the long term, highlighting the importance of native mammal population retention outside of the reserve system.

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Supplementary Information

Stable isotope analysis of land-snail shells

Background

Land snails precipitate aragonitic shells in isotopic equilibrium with the bicarbonate pool of body waters. Stable carbon and oxygen isotope compositions of respired CO^2 and body water, which determine $\delta^{13}C$ and $\delta^{18}O$ of the bicarbonate pool, appear in turn to be influenced by a variety of external environmental parameters (Goodfriend *et al*. 1989). Precise relationships governing land-snail shell stable isotopes and environmental conditions has been the subject of considerable debate over the years. While land-snail shell carbon isotopes are regarded by the majority to be related to those of snail diet (usually comprised of local vegetation with minor contributions from limestone substrates (Francey 1983; Goodfriend and Hood 1983; Goodfriend *et al*. 1989), the factors determining land-snail shell oxygen isotopes appear much more complicated. Previous empirical studies of modern land snails have shown $\delta^{18}O$ values of shell aragonite ($\delta^{18}O_{shell}$) to be related to rainfall $\delta^{18}O$ values ($\delta^{18}O_{rain}$), and in arid environments, also to relative humidity (h) (Yapp 1979; Margaritz *et al*. 1981; Goodfriend *et al*. 1989; Balakrishnan *et al*. 2005). In addition to this, Balakrishnan and Yapp (2004) find stable isotopes of land-snail shells are also influenced by temperature, the $\delta^{18}O$ of ambient water vapor and snail physiologies.

Sampling and cleaning protocols

Forty-three fossil and six modern land snail (*Cupedora* spp.) shells from the KHC fossil assemblage and surface environs were analysed for stable isotopes. The state of preservation of the fossil land snails appeared exceptional, with no signs of recrystallization of the primary aragonite tests to calcite. Shells were cleaned by first soaking overnight in 3% H_2O_2 to remove organics. The H_2O_2 reagent was then changed, and shells placed in an ultrasonic bath for three 10-minute sessions, followed by repeated rinsing in demineralized water. Cleaned shells were then dried overnight at 60°C. Sediment grains that still adhered to shells after the cleaning process were mechanically removed using a small scalpel blade (following Prideaux 2010). Cleaned shell samples were then crushed to a fine powder using an agate mortar and pestle. Powdered shell samples (~200μg) were reacted at 90°C in a Kiel carbonate device and analysed on a Finnigan MAT251 mass spectrometer. Isotope results were standardised to the Vienna-Peedee Belemnite (V-PDB) scale by in-run comparison to NBS-19 and NBS-18. $\delta^{13}C$, $\delta^{18}O$ ‰ = $[(R_{sample} / R_{standard}) - 1] \times 1000$, where R is the $^{13}C/^{12}C$ or $^{18}O/^{16}O$ ratio. Reproducibility of $\delta^{13}C$ and $\delta^{18}O$ for NBS-19 (n=11) during the period of analysis was ± 0.02 (1σ)‰ and ± 0.03‰, respectively.

Table S1: Summary of body mass, ecological niche and distribution characteristics of mammal fauna of the Kelly Hill Cave (5K1) fossil assemblage, Kangaroo Island, South Australia. Compiled from Van Dyck and Strahan (2008) with additional sources listed where applicable (after Macken *et al*. 2012).

Species	Common name	Body weight	Status	Distribution	Climate	Habitat	Lifestyle	Activity	Diet	References
Tachyglossus aculeatus	Short-beaked Echidna	2–7kg	Common	Australia wide	Broad range	broad range	Ground dwelling	Diurnal	Ants and termites	
Antechinus flavipes	Yellow footed antechinus	34–56g	Abundant over range	Southern Australia	Temperate, semi-arid	Closed and tall open forests and woodlands; open heath and swamps.	Ground dwelling, tree hollow nesting, fossorial.	Nocturnal	Invertebrates, flowers, nectar, small vertebrates.	Lada *et al*. (2008).
Dasyurus maculatus	Spotted-tailed Quoll	900–5000g	Rare, limited. Extinct in SA	Coastal distribution along Eastern Australia, Tasmania, formerly Vic, SE SA and Kangaroo Island	Tropical to temperate	Rainforest, wet and dry sclerophyll forest, woodland, coastal scrub and heath	Ground dwelling	Nocturnal	Invertebrates, small and medium vertebrates, carrion. (Adult diet mainly medium vertebrates)	
Dasyurus viverrinus	Eastern Quoll	700–1900g	Locally extinct, restricted to Tasmania.	Tasmania, formerly Eastern NSW, Vic and SE SA including Kangaroo Island	Semi-arid, temperate, tropical to alpine	Open forest and woodland, open grasslands and alpine heath	Ground dwelling	Nocturnal	Invertebrates, small vertebrates (reptiles, mammals, birds), berries, carrion.	
Phascogale tapoatafa	Brush tailed Phascogale	106–311g	Patchy, sparse populations	Coastal distribution along Eastern Australia, NW WA and SW WA. SE SA coast.	Tropical and Temperate	Broad range, but thought to prefer dry sclerophyll forest-woodland, open forest with sparse understorey	Arboreal (mature trees)	Nocturnal	Large invertebrates, nectar.	

Species	Common name	Body weight	Status	Distribution	Climate	Habitat	Lifestyle	Activity	Diet	References
Sarcophilus harrisii	Tasmanian Devil	5–14kg	Vulnerable. Restricted to Tasmania.	Tasmania	Semi-arid, temperate, tropical to alpine	Eucalypt forest, grassy woodland and coastal scrub	Ground dwelling	Nocturnal	Large vertebrates	
Sminthopsis aitkeni	Kangaroo Island Dunnart	86–106g	Endangered. Restricted to Kangaroo Island	Kangaroo Island	Mediterranean	Mallee heath	Ground dwelling	Nocturnal	Invertebrates (spiders , crickets, cockroaches)	
Sminthopsis crassicaudata	Fat tailed Dunnart	10–20g	Common	Widespread over Southern and Central Australia.	Arid, semi-arid, temperate.	Open woodland, low shrublands, tussock grasslands.	Ground dwelling	Nocturnal	Invertebrates (cockroaches, spiders, beetles)	
Sminthopsis murina	Common Dunnart	10–28g	Common over range	Widespread over NSW, Vic, SE Qld and Eastern SA.	Semi-arid, temperate and tropical.	Woodland, open forest and heath.	Ground dwelling	Nocturnal	Invertebrates (beetles, spiders, cockroaches, cricket larvae).	
Isoodon obesulus	Southern Brown Bandicoot	400–1850g	Endangered	Restricted to isolated localities SW WA, Kangaroo Island, Fleurieu Peninsula and Lower SE SA, Coastal Vic and Tasmania.	Temperate	Forest, woodland, shrub and heath.	Ground dwelling and fossorial.	Diurnal	Invertebrates, fungi.	Short *et al.* (1998)
Perameles bougainville	Western Barred Bandicoot	165–379g	Endangered	Formerly across Southern Australia, now restricted to island populations off WA coast.	Semi-arid	Dense scrub, saltbush/blue bush heath, river plains, vegetated coastal dunes.	Ground dwelling	Nocturnal	Invertebrates, seeds and berries.	Short *et al.* (1998)
Perameles gunnii	Eastern barred bandicoot	500–1450g	Endangered	Tasmania and restricted on mainland to four re–introduced colonies in SW Vic, formerly SE SA and SW Vic.	Temperate	Open forest, heath and grassland.	Ground dwelling, shelters in dense ground cover, fossorial.	Nocturnal	Invertebrates, worms, fungi, bulbs, tubers, fruits.	Dufty (1994); Mallick *et al.* (1997)
Acrobates pygmaeus	Feathertail Glider	10–15g	Not listed	Eastern Australia	Temperate	Tall forest and woodland	Arboreal	Nocturnal	Nectar, pollen, insects	

Species	Common name	Body weight	Status	Distribution	Climate	Habitat	Lifestyle	Activity	Diet	References
Cercartetus concinnus	Western Pygmy-possum	8–21g	Not listed	Southern Australia	Mediterranean	Mallee woodland, heath, and dry sclerophyll forest	Arboreal	Nocturnal	Nectar, pollen (*Banksia, Hakea, Grevillea, Eucalyptus, Melaleuca*), insects	
Cercartetus lepidus	Little Pygmy-possum	6–10g	Not listed	Kangaroo Island, SE SA, NW Vic, Tasmania.	Mediterranean	Dry to wet sclerophyll forest and woodland, sedgeland, mallee, dry heath	Arboreal	Nocturnal	Nectar, pollen, insects	
Cercartetus nanus	Eastern Pygmy–possum	15–43g	Not listed	SE SA, Vic, Eastern NSW and Blue Mountains.	Temperate, tropical.	Closed and open forests, woodlands.	Arboreal and ground foraging.	Nocturnal	Nectar, pollen (*Banksia, Eucalyptus, Callistemon*), insects.	
Pseudocheirus peregrinus	Common Ringtail Possum	700–900g	Common	SE SA, Eastern Australia to top Qld.	Temperate, tropical.	Tall, open and closed forests and woodlands.	Arboreal	Nocturnal	Leaves, flowers, fruits.	
Trichosurus vulpecula	Common Brushtail Possum	1.2–4.5kg	Abundant in south-eastern Australia, Kangaroo Island and Tasmania, declining elsewhere	Northern, eastern and south-western Australia. Formerly throughout arid Australia	Arid, temperate, tropical, alpine.	Almost any, but prefers dry eucalyptus forest and woodland	Arboreal and ground foraging.	Nocturnal	Leaves, flowers, fruits.	
Bettongia lesueur	Burrowing Bettong	680–2180g	Common on Barrow, Bernier and Dorre Islands. Extinct on mainland Australia	Barrow, Bernier and Dorre Islands. Formerly WA, NT, SA (excluding SE and Kangaroo Island), western NSW and south-western Qld	Arid, semi-arid zones	Most habitats excluding those with dense vegetation and higher rainfall	Ground dwelling, fossorial	Nocturnal	Underground fungi, fruit, seed, tubers, roots, bulbs, some plants, arthropods.	

Species	Common name	Body weight	Status	Distribution	Climate	Habitat	Lifestyle	Activity	Diet	References
Bettongia penicillata	Brush-tailed Bettong	750-1850g	Rare, *Bettongia penicillata penicillata* extinct	Wheat belt, Western Australia, formerly arid and semiarid WA, NT, SA, NSW and Vic	Arid, semi-arid zones	Open forest, woodland and scrub. Remaining populations associated with *Gastrolobium* thickets	Ground dwelling	Nocturnal	Underground fungi, tubers, bulbs, seed	
Potorous platyops	Broad–faced Potoroo	700g	Extinct	Coastal from SA to WA.	Temperate.	Forest with dense understorey.	Ground dwelling	unknown	Unknown but expected to be similar to *P. tridactylus.*	
Potorous tridactylus	Long–nosed Potoroo	660–1640g	Vulnerable	East Coast, NSW, Vic, southern Qld, Tasmania.	Rainfall >760mm	Coastal heath, dry and wet sclerophyll forest, requires thick groundcover.	Ground dwelling	Nocturnal	Fungi, arthropods, fruits, plant tissues and seeds.	Holland and Bennett (2007)
Lasiorhinus latifrons	Southern Hairy-nosed wombat	17.5–36kg	Common, limited	Nullarbor Plain, Eyre Peninsula and Murray-Mallee	Arid, semi-arid zones	Semiarid grassland	Ground dwelling, semi-fossorial	Nocturnal	Native perennial grasses, forbes and introduced Thread Iris (*Gynandriris setifolia*)	
Phascolarctos cinereus	Koala	7–14.9kg	Common	Eastern Qld, NSW, Vic, SE SA. Introduced populations in SA.	Temperate, tropical.	Eucalypt forest and woodland	Arboreal	Nocturnal	*Eucalyptus*	
Lagorchestes leporides	Eastern Hair-wallaby	3.1kg	Extinct	Central NSW, NW Vic, E SA	Unknown	Plains	Ground dwelling	Unknown	Unknown	Prideaux *et al.* (2007)
Macropus eugenii	Tammar Wallaby	4-10kg	Common	SW WA, Kangaroo Island, formerly Southern SA	Mediterranean	Coastal scrub, heath, dry sclerophyll forest, mallee and woodland. Requires dense low vegetation and open grassland for feeding	Ground dwelling	Nocturnal	Grazer	

Species	Common name	Body weight	Status	Distribution	Climate	Habitat	Lifestyle	Activity	Diet	References
Macropus fuliginosus	Western Grey Kangaroo	17–85kg	Widespread and common.	Southern and eastern Australia.	Broad, temperate to tropical and semi-arid.	Sclerophyll forest, woodland, shrubland and heathland.	Ground dwelling	Nocturnal	Predominantly short grass grazer but can browse on small shrubs, soft herbs and ferns.	
Macropus greyi	Toolache Wallaby	Unknown but > 5kg	Extinct	SE SA.	Temperate	Stringybark heath associated with grasslands and swampy regions.	Ground dwelling	Nocturnal	Grazer	
Macropus rufogriseus	Red–necked Wallaby	12–23.7kg	Common	SE SA, SW Vic, Tasmania, eastern Australia.	Alpine, temperate, sub-tropical.	*Eucalyptus* forest, closed heath, sedges.	Ground dwelling	Nocturnal	Grasses and herbs, seed heads, occasional browse of small shrubs and seedlings.	Le Mar and McArthur (2005)
Onychogalea fraenata	Bridled Nailtail Wallaby	4–8kg	Endangered	Central Qld. Formerly slopes and plains west of the Great Dividing Range and along the Murray River	Semi-arid	Shelters in open forest, tall shrubland, feeds in grassy woodland	Ground dwelling	Nocturnal	Mixed forbes (chenopod and soft-leaved grasses), grass and browse	
Lagostrophus fasciatus	Banded Hair-wallaby	1–2.3kg	Extinct on mainland	Bernier and Dorre Islands, formerly southern Australia	Semi-arid	Woodland with dense scrub on sandplains	Ground dwelling	Nocturnal	Grazer/browser	Short and Turner (1992)
‘Procoptodon’ browneorum	-	50kg	Extinct	SE SA, Nullarbor, NE NSW.	Wide range.	Wide range.	Ground dwelling	Unknown	Browse or mixed feeding.	Prideaux (2004); Helgen *et al.* (2006); Johnson (2006)
‘Procoptodon’ gilli	-	43–77kg	Extinct	SE Australia.	Temperate	Forest, woodland.	Ground dwelling	Unknown	Browse	Prideaux (2004), Helgen *et al.* (2006), Johnson (2006)

Species	**Common name**	**Body weight**	**Status**	**Distribution**	**Climate**	**Habitat**	**Lifestyle**	**Activity**	**Diet**	**References**
Hydromys chrysogaster	Water Rat	340–1275g	Sparse to common across range	Widespread over eastern Australia, SE SA, Central Qld, northern NT and SW coast WA.	Tropical, temperate, semi-arid, sub alpine.	Requires permanent fresh or brackish water though can occupy marine environments	Aquatic, ground dwelling	Diurnal	Aquatic invertebrates, fish, crustaceans and small vertebrates.	
Mastacomys fuscus	Broad–toothed Rat	97–145g	Vulnerable to endangered.	Snowy mountains, Victorian alps, and Barrington tops, Tasmania. Formerly SE SA and Coorong.	Alpine, subalpine. High rainfall, cool to cold winter.	Wet sclerophyll forest with dense undergrowth and wet sedgelands and heathlands.	Ground dwelling	Noctidiurnal	Grasses, some shrub leaves.	Watts and Aslin (1981)
Notomys mitchellii	Mitchell's Hopping Mouse	40–60g	Common	Semiarid zone of WA through SA and Vic.	Semi-arid, arid	Mallee/Eucalypt woodland, dune fields. Variable understorey density.	Ground dwelling	Nocturnal	Shrubs, roots and leaves.	
Pseudomys apodemoides	Silky Mouse	16–22g	Common	SE SA, western Victoria	Semi-arid, temperate.	Dry mallee-heathlands, sand dunes and plains.	Ground dwelling	Diurnal	Banksia nectar, seeds, invertebrates (cockroaches).	Cockburn (1981); Seebeck and Menkhorst (2000)
Pseudomys auritus	Long–eared Mouse	100g	Extinct	SE SA, western Victoria	Temperate, semi-arid.	Probably open heath, dense mallee, open scrub, woodland and dense understorey forest.	Ground dwelling	Unknown	Unknown	
Pseudomys australis	Plains Mouse	30–65g	Vulnerable	Restricted to central SA, formerly widespread over Murray Darling Basin in SA, Nullarbor plain and SW Qld.	Arid, semi-arid.	Cracking clay pans and arid gibber plains	Ground dwelling	Nocturnal	Seeds, plant material, insects.	
Pseudomys gouldii	Gould's Mouse	50g	Extinct	NSW, Eastern SA. West coast WA.	Temperate, semi-arid	Hummock grasslands.	Ground dwelling	Unknown	Unknown	

Species	Common name	Body weight	Status	Distribution	Climate	Habitat	Lifestyle	Activity	Diet	References
Pseudomys occidentalis	Western Mouse	33–53g	Common	South-west WA. Formerly southern SA	Temperate, semi-arid	Low shrubland, sparse to dense shrub mallee, mid-dense woodland. Prefers long unburnt dense vegetation.	Ground dwelling	Nocturnal	Fibrous plant material, invertebrates	
Pseudomys shortridgei	Heath Mouse	55–90g	Vulnerable	Formerly SW coastal WA, introduced to southern SA. Remaining populations on KI and Lower SE SA, Grampians.	Temperate, semi-arid.	Early- to mid-successional dry heathland, Stringybark open forest with heath understorey, mallee and mallee heath.	Ground dwelling	Nocturnal	Seeds, flowers, berries, tubers, fungi, grass stems and leaves.	Seebeck and Menkhorst (2000); Kemper *et al*. (2010)
Rattus fuscipes	Bush Rat	40–225g	Common across range	Coastal distribution SW WA, southern SA, SE SA, eastern Vic, NSW and wet tropics Qld.	Temperate to tropical.	Coastal forest and scrub, subalpine woodland, *Eucalyptus* forest, rainforest with dense shrub understorey.	Ground dwelling, arboreal.	Nocturnal	Fungi, stems, leaves, insects, fruits, flowers and seeds.	Ford *et al.* (2003); Holland and Bennett (2007)
Rattus lutreolus	Swamp Rat	50–200g	Common	Fleurieu Peninsula, KI, SE SA, southern Vic, eastern Australia and Tasmania.	Temperate, tropical.	Coastal vegetation, wet dense heath, grass and sedge, wet and dry sclerophyll forest.	Ground dwelling	Nocturnal	Grasses and sedges, fruits, seeds, arthropods.	Fox and Monamy (2007); Holland and Bennett (2007)

Table S2. Number of identified specimens (NISP) of mammals excavated from Kelly Hill Cave (5K1)

Units	7	6	5	4	3	2	1a	1b	1c
Layers	15	14	13	12	11	10	9	8-7	6-4
Tachyglossus aculeatus	0	0	0	0	0	0	0	0	1
Antechinus flavipes	3	1	13	2	3	1	0	0	0
Antechinus sp. indet.	0	0	0	2	0	0	0	0	6
Dasyurus maculatus	0	0	0	2	10	9	2	6	7
Dasyurus viverrinus	0	0	1	3	17	18	5	19	9
Dasyurus sp. indet.	1	0	2	0	3	0	0	0	5
Phascogale tapoatafa	0	1	1	0	0	1	0	0	1
Phascogale sp. indet.	0	0	1	0	0	1	0	0	0
Sarcophilus harrisii	0	0	1	0	1	3	2	2	6
Sminthopsis aitkeni	3	0	6	7	24	75	6	13	13
Sminthopsis crassicaudata	0	0	1	1	10	1	0	1	0
Sminthopsis murina	0	0	0	0	2	4	0	1	1
Sminthopsis sp. indet.	3	0	20	19	34	22	2	7	17
Isoodon obesulus	0	2	0	0	13	13	8	15	15
Perameles bougainville	4	5	14	6	19	24	0	8	8
Perameles sp. cf. *P. bougainville*	3	0	9	0	0	0	0	0	0
Perameles gunnii	0	0	6	2	1	0	0	0	0
Perameles sp. indet.	0	0	9	0	0	0	0	0	0
Acrobates pygmaeus	0	0	0	0	1	3	0	0	3
Cercartetus concinnus	0	0	0	2	2	4	0	9	26
Cercartetus lepidus	1	0	3	3	38	10	2	4	3
Cercartetus nanus	1	0	7	0	0	0	0	0	3
Pseudocheirus peregrinus	1	0	4	0	0	0	0	0	0
Trichosurus vulpecula	0	0	0	0	0	3	0	2	1
Bettongia lesueur	0	0	2	6	4	0	0	0	0
Bettongia sp. cf. *B. lesueur*	0	0	1	0	0	0	0	0	0
Bettongia penicillata	0	0	0	3	1	0	1	2	0
Bettongia sp. indet.	0	0	1	0	2	0	1	1	1
Potorous platyops	0	0	14	17	41	49	7	31	14
Potorous tridactylus	5	1	12	0	1	0	0	0	0
Potorous sp. indet.	0	0	2	0	0	0	0	0	0
Phascolarctos cinereus	0	0	2	0	0	0	0	0	0
Lagorchestes leporides	0	0	0	0	0	3	0	2	0
Macropus eugenii	0	0	0	0	0	4	18	7	6
Macropus fuliginosus	2	0	26	2	0	8	5	5	12
Macropus sp. cf. *M. fuliginosus*	7	3	0	0	0	0	0	0	0
Macropus greyi	2	0	14	1	0	1	0	1	0
Macropus rufogriseus	0	0	19	5	5	0	0	0	1
Macropus sp. indet.	14	4	18	0	4	0	0	2	0
Onychogalea fraenata	0	0	1	0	1	22	19	65	28
Onychogalea sp. indet.	0	0	0	0	0	0	0	1	0
Lagostrophus fasciatus	0	0	0	0	0	0	0	0	1
‘*Procoptodon*’ *browneorum*	1	0	0	0	0	0	0	0	0

Table S2 cont.

Units	7	6	5	4	3	2	1a	1b	1c
Layers	15	14	13	12	11	10	9	8-7	6-4
‘*Procoptodon*’ *gilli*	3	0	17	4	0	0	0	0	0
‘*Procoptodon*’ sp. indet.	0	0	1	0	0	0	0	0	0
Hydromys chrysogaster	0	0	1	0	1	0	0	0	0
Mastacomys fuscus	1	5	7	18	73	30	2	20	12
Notomys mitchellii	0	0	0	0	25	19	0	3	0
Pseudomys apodemoides	14	5	54	17	11	3	1	1	1
Pseudomys auritus	0	0	1	4	54	15	0	15	7
Pseudomys australis	0	1	5	57	349	209	36	70	50
Pseudomys gouldii	0	0	0	1	0	0	0	1	1
Pseudomys occidentalis	23	2	62	152	818	831	107	197	119
Pseudomys shortridgei	7	0	7	47	440	598	96	164	74
Pseudomys sp. indet.	0	0	6	17	114	37	0	4	7
Rattus fuscipes	54	18	341	195	816	880	142	395	190
Rattus lutreolus	18	11	60	18	68	54	2	7	20
Rattus sp. indet.	0	0	9	0	0	0	0	0	0
Total	171	59	781	613	3006	2955	464	1081	669

Table S3. Radiocarbon results and age estimates of bones dated from the Kelly Hill Cave (5K1) excavation.

Lab Code	**Layer and spit**	**Unit**	**C:N (atomic)**	**δ^{13}C (‰)**	**^{14} C Age kyr BP**	**Calibrated Age cal. kyr BP[1]**
NZA 33928	1(S1)	1a	-	-22.6	7.12 ± 0.04	7.97-7.80 (95.4%)
OZN779	3(S1)	1a	3.4	-21.4	8.79 ±0.05	9.90-9.55 (95.4%)
NZA 33933	5(S1)	1a	-	-22.6	6.03 ± 0.04	6.94-6.68 (95.4%)
OZN781	5(S1)	1a	3.3	-22.9	6.6±0.04	7.57-7.43 (95.4%)
OZN784	6(S1)	1a	3.2	-21.8	6.51±0.05	7.44-7.27 (95.4%)
OZN786	7x(S1)	1b	3.4	-21.8	6.83±0.05	7.69-7.56 (93.2%) 7.54-7.52 (2.2%)
OZN787	7y(S1)	1b	3.3	-23.0	6.79±0.05	7.68-7.50 (95.4%)
OZN788	8(S1)	1b	3.4	-21.8	7.16±0.06	8.04-7.79 (95.4%)
NZA 33932	8(S2)	1b	-	-22.6	7.98±0.04	8.98-8.60 (95.0%)
OZO528	9(S1)	1c	3.2	-22.7	8.97±0.05	10.21-9.79 (95.4%)
OZO531	10(S1)	2	3.5	-21.8	13.58±0.07	16.94-16.48 (95.4%)
NZA 33977	10(S2)	2	-	-22.0	8.41±0.05	9.49-9.25 (93.8%) 9.17-9.15 (1.6%)
Beta-320117	10(S2)	2	-	-17.6	19.61±0.08	23.65-23.33 (95%)
OZO532	10(S3)	2	3.5	-17.5	14.30±0.08	17.75-17.03 (95.4%)
OZN793	11(S3)	3	3.2	-17.0	16.28±0.08	19.81-19.72 (4.1%) 19.59-19.24 (85.4%) 19.10-18.95 (5.9%)

Lab Codes: OZ = ANSTO, NZA = Rafter Radiocarbon, Beta = Beta Analytic.

[1] Calibrated age ranges and corresponding probability distribution function area percentages after projection of radiocarbon measurements onto calibration curves using the OxCal 4.1.7 programme (Bronk Ramsey 2009). Radiocarbon ages < 11.0 cal kyr BP were calibrated using the SHCal04 calibration curve (McCormac *et al*. 2004). Radiocarbon ages > 11.0 cal kyr BP were calibrated using the IntCal09 calibration curve (Reimer *et al*. 2009).

Table S4. U and Th results and ages estimates of speleothems from the Kelly Hill Cave (5K1) excavation and nearby chamber in Kelly Hill Caves.

Lab Code	**Layer and spit**	**Unit**	**U conc. (ppb)**	**$^{230}Th/^{232}Th^{1}$**	**$^{230}Th/^{238}U$**	**$^{234}U/^{238}U$**	**Age^{2} (kyr)**	**Age$_{corr.}^{3}$ (kyr)**	**$^{234}U/^{238}U_{corr.\ initial}$**
UMD120309-215	5(S3)	1a	80	7	0.070 ± 0.001	1.077 ± 0.003	7.29 ± 0.08	6.9 ± 0.4	1.099 ± 0.003
UMD120309-217	6(S1)	1a	90	9	0.073 ± 0.001	1.079 ± 0.003	7.69 ± 0.05	7.4 ± 0.3	1.102 ± 0.003
UMD120309-225	8(S1)^{T}	1b	120	7	0.073 ± 0.001	1.074 ± 0.003	7.7 ± 0.1	7.3 ± 0.5	1.097 ± 0.003
UMD120309-226	8(S1)^{B}	1b	70	3	0.091 ± 0.003	1.065 ± 0.005	9.7 ± 0.3	9 ± 1	1.091 ± 0.006
UMD120309-242	9(S1)^{T}	1c	60	11	0.105 ± 0.002	1.077 ± 0.003	11.2 ± 0.2	10.8 ± 0.5	1.110 ± 0.004
UMD120309-302	9(S1)^{B}	1c	130	9	0.096 ± 0.001	1.085 ± 0.003	10.10 ± 0.07	9.69 ± 0.41	1.116 ± 0.003
UMD120309-311	11(S1)	3	260	40	0.0997 ± 0.0008	1.102 ± 0.002	10.34 ± 0.03	10.25 ± 0.07	1.134 ± 0.003
UMD120309-312	11(S5)	3	8	6	0.181 ± 0.002	1.094 ± 0.003	19.7 ± 0.2	19 ± 1	1.152 ± 0.005
KH SC S-1a	–	–	120	0.4	0.006 ± 0.001	1.0515 ± 0.0007	0.62 ± 0.03	–	–

[1.] All U and Th ratios are given as activity ratios. [2.] Ages calculated using the half-lives for ^{230}Th (75.69±0.023 kyr) and ^{234}U (245.25±0.049 kyr) of Cheng *et al*. (2000). [3] Corrections for detrital ^{230}Th made using $^{230}Th/^{232}Th_{initial}$ = 0.4 ± 0.4 estimated from modern stalagmite sample KH SC S-1a. ^{T} = tip and ^{B} = base of stalagmite. Spits are 5 cm sections of sediment excavated within stratigraphic layers.

Table S5. Raw δ^{13}C and δ^{18}O from modern and fossil land snail shells utilized in this study.

Sample ID	Species	Unit/ Age	Layer	δ^{13}C V-PDB (‰)	δ^{18}O V-PDB (‰)
K1-2571a	*Cupedora sutilosa*	Modern	-	-7.9	1.6
K1-2571b	*Cupedora sutilosa*	Modern	-	-9.4	-0.6
K1-2571c	*Cupedora sutilosa*	Modern	-	-9.6	0.2
K1-2572a	*Cupedora tomsetti*	Modern	-	-9.2	0.8
K1-2572b	*Cupedora tomsetti*	Modern	-	-9.3	1.0
K1-2572c	*Cupedora tomsetti*	Modern	-	-9.5	1.0
K1-149	*Cupedora tomsetti*	1a	1	-6.1	0.2
K1-906	*Cupedora sutilosa*	1a	1	-7.7	0.8
K1-907	*Cupedora* sp. indet.	1a	1	-9.0	0.6
K1-0707	*Cupedora* sp. indet.	1a	2	-8.4	1.1
K1-1269	*Cupedora sutilosa*	1a	2	-8.6	-0.2
K1-320	*Cupedora tomsetti*	1a	2	-6.1	1.2
K1-336	*Cupedora tomsetti*	1a	2	-9.1	0.2
K1-681	*Cupedora tomsetti*	1a	2	-14.1	-0.2
K1-271	*Cupedora tomsetti*	1a	3	-6.4	1.4
K1-722	*Cupedora sutilosa*	1a	3	-10.6	-0.9
K1-746	*Cupedora sutilosa*	1a	3	-9.9	-0.1
K1-384	*Cupedora sutilosa*	1a	4	-6.9	-0.1
K1-761	*Cupedora sutilosa*	1a	4	-6.7	0.0
K1-853	*Cupedora tomsetti*	1a	4	-8.9	0.9
K1-801	*Cupedora tomsetti*	1a	5	-6.0	1.7
K1-930	*Cupedora sutilosa*	1a	5	-7.9	0.8
K1-2405	*Cupedora sutilosa*	1a	5	-8.9	0.5
K1-355	*Cupedora sutilosa*	1a	6	-6.6	0.6
K1-842	*Cupedora sutilosa*	1a	6	-5.6	0.1
K1-1265	*Cupedora sutilosa*	1a	6	-8.1	0.8
K1-619	*Cupedora sutilosa*	1b	7	-7.2	0.4
K1-635	*Cupedora sutilosa*	1b	7	-6.1	0.5
K1-973	*Cupedora tomsetti*	1b	7	-8.0	1.1
K1-479	*Cupedora sutilosa*	1b	8	-7.2	1.0
K1-1041	*Cupedora tomsetti*	1b	8	-6.8	1.2
K1-1274	*Cupedora tomsetti*	1b	8	-7.3	1.2
K1-426	*Cupedora tomsetti*	1c	9	-6.1	1.3
K1-1150	*Cupedora sutilosa*	1c	9	-10.4	0.1
K1-1151	*Cupedora tomsetti*	1c	9	-9.0	0.7
K1-0070	*Cupedora tomsetti*	2	10	-8.5	
K1-1408	*Cupedora* sp. indet.	3	11	-8.7	1.5
K1-1662	*Cupedora* sp. indet.	3	11	-9.9	6.1
K1-1811	*Cupedora tomsetti*	3	11	-11.8	-0.3
K1-1852	*Cupedora* sp. indet.	4	12	-9.1	-0.2
K1-1891	*Cupedora sutilosa*	4	12	-7.3	0.7
K1-1892	*Cupedora tomsetti*	4	12	-7.0	2.5
K1-2068	*Cupedora* sp. indet.	5	13	-6.6	0.2
K1-2150	*Cupedora sutilosa*	5	13	-5.8	0.7
K1-2219	*Cupedora* sp. indet.	5	13	-7.0	0.8
K1-2313	*Cupedora* sp. indet.	6	14	-8.2	-0.1
K1-2350	*Cupedora* sp. indet.	7	15	-6.1	-0.1
K1-2374	*Cupedora* sp. indet.	7	15	-6.2	0.5
K1-2394	*Cupedora* sp. indet.	7	15	-6.1	0.7

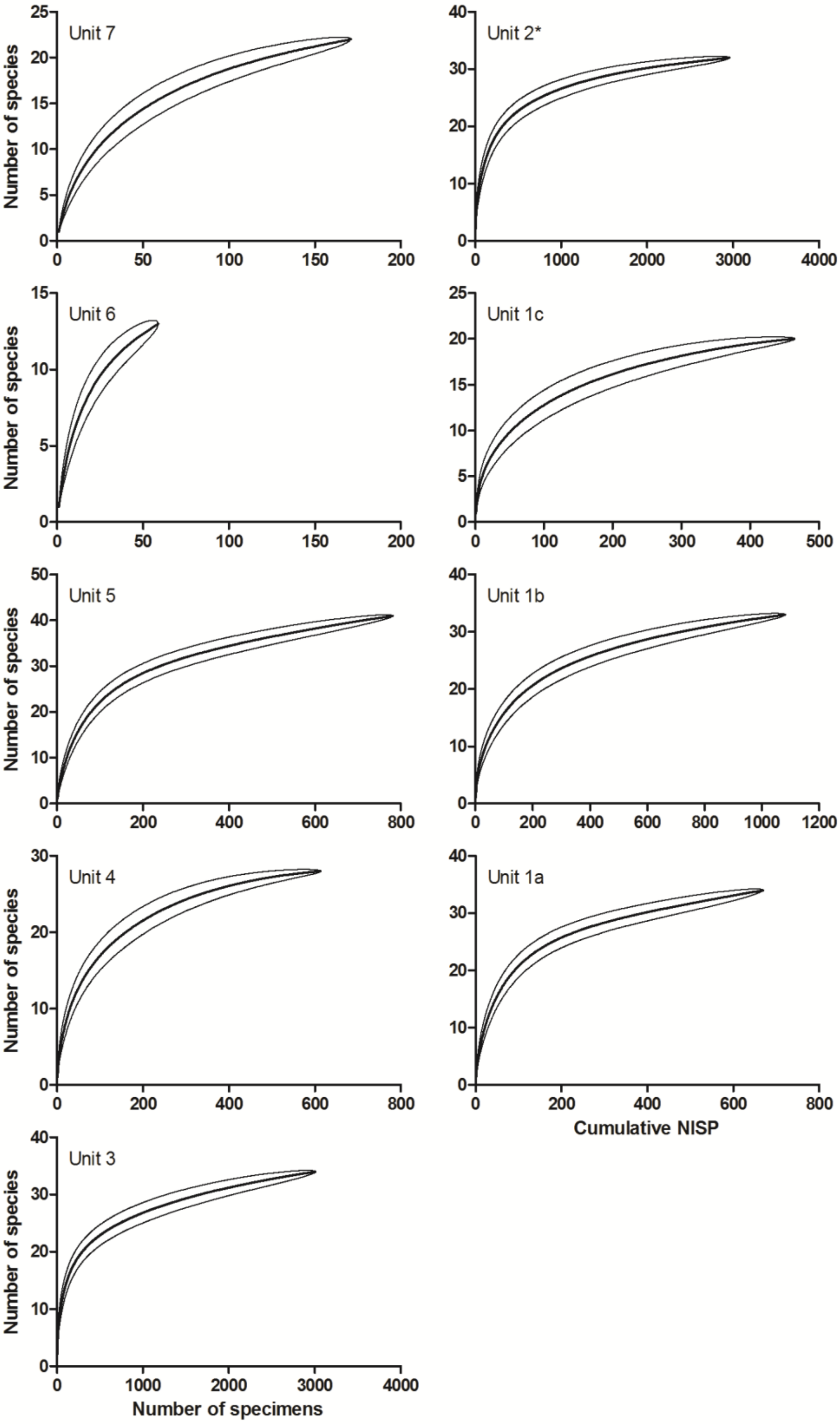

Fig. S1. Rarefaction curves for each Kelly Hill Cave (5K1) sedimentary unit and sub-unit showing that with the exception of Unit 6, sample sizes are large enough to include all but the rarest of species. * = reworked.

Fig.S2: Associated macropodid partial skeleton excavated from Kelly Hill Cave (5K1), Kangaroo Island

Fig. S3: Articulated macropodid hind limb excavated from Kelly Hill Cave (5K1), Kangaroo Island

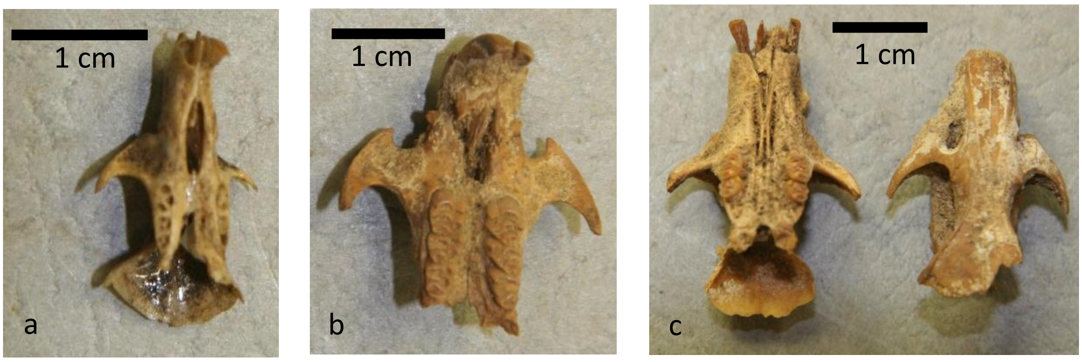

Fig.S4: Splanchnocrania of a. *Pseudomys occidentalis*, b. *Mastycomys fuscus* and c. *Rattus lutreolus* excavated from Kelly Hill Cave (5K1), Kangaroo Island

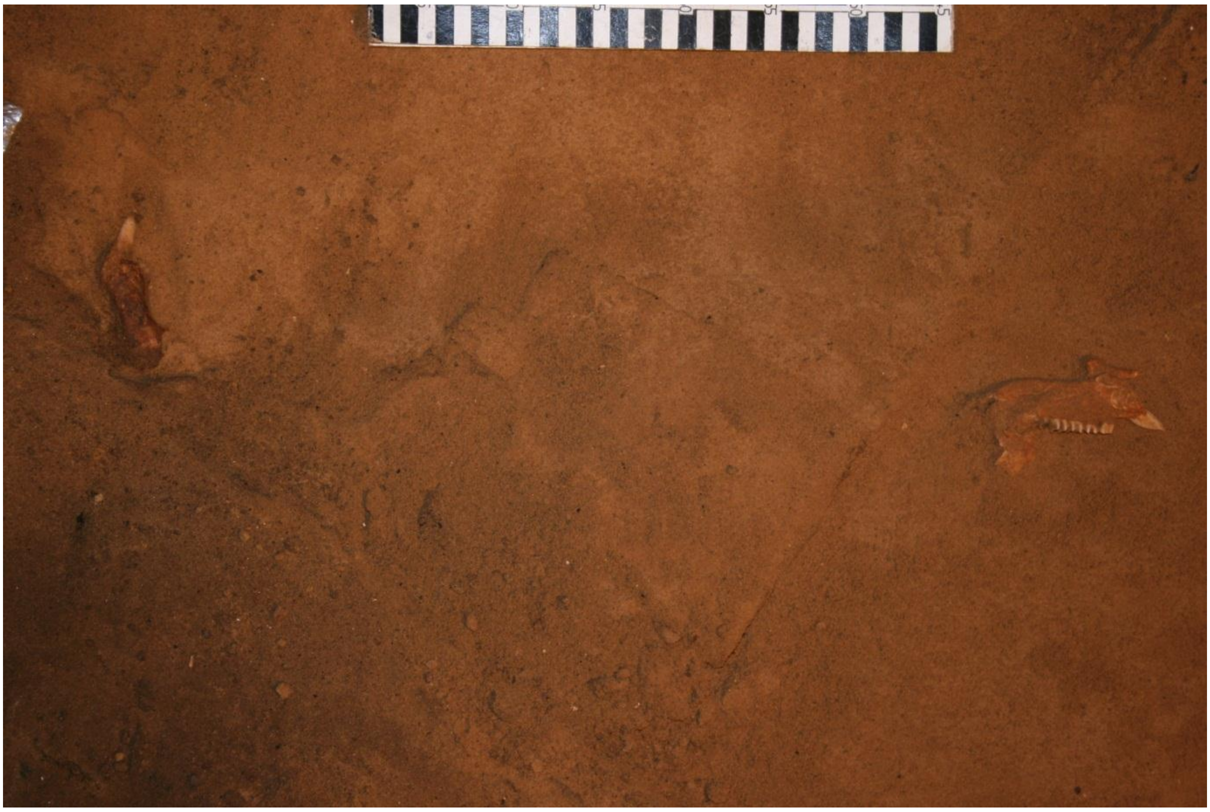

Fig. S5: Associated ‘*Procpotodon*’ *gilli* dentaries excavated from Kelly Hill Cave (5K1), Kangaroo Island

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CHAPTER 8

General Discussion

As each chapter of this thesis has been prepared in manuscript format, each includes a discussion of the data interrogated. The following is a summary and discussion of the main finding of each published paper or manuscript, followed by a discussion of the work as a whole.

Seton Rockshelter

As KI's only pre-existing fossil collection covering the time period of interest, the palaeontological component of the Seton Rockshelter assemblage was reviewed and discussed in chapter 2. Some specimens were re-identified, but most corrections arose from advances in taxonomy. Five additional radiocarbon dates were obtained from bone stored in the South Australian Museum's Palaeontology Collection. All calibrated ages including charcoal dates reported by J. Hope *et al*. (1977) occurred in stratigraphic order demonstrating high unlikelihood that the assemblage has been reworked. Analysis suggests that the base of the assemblage was primarily accumulated by *Sarcophilus harrisii* and *Tyto alba*. Stone tools indicate that humans used the shelter only occasionally until about 17 kyr ago, at which time human use intensified. This change in accumulation agent coincided with J. Hope *et al*.'s (1977) interpretation of climate change making it impossible to determine which variable was responsible for apparent faunal change.

The Seton assemblage includes three fragmentary specimens of '*P.*' *gilli* and one of '*P.*' *browneorum*. Previous researchers (Baynes 1999, Kershaw *et al.* 2000; Roberts *et al.*2001; Gillespie *et al.* 2006, 2012; Brook *et al.* 2007) argue that the fragmentary nature of the specimens indicated reworking. However, all of the fossil specimens from the site are highly fragmented and radiocarbon dating indicates that the assemblage is *in situ*. Therefore, the most parsimonious interpretation of the available evidence is that the assemblage, including megafauna, is probably *in situ*. However, as the age of the Seton megafauna cannot be corroborated by direct dating, it is suggested that Seton rockshelter should be excluded from future megafauna extinction debate until the site has been re-excavated and fresh specimens have been dated using multiple cutting-edge techniques to seek an age consensus.

Black Creek Swamp and KHC assemblages also include remains of '*P.*' *gilli* and '*P.*' *browneorum*. Multiple dating techniques have been applied to the Black Creek Swamp assemblage (Wells *et al*. 2006) and provide a minimum age of 45 kyr BP. Sthenurine kangaroos occur in unit 7 of the KHC excavation. Due to bone collagen degradation and the absence of charcoal and speleothem this unit has not yet been dated. However, unit 3 has been dated at around 20 kyr old by radiocarbon and U–Th dating, suggesting that the sthenurines from unit 7 are much older than the Seton specimens. Therefore, the Black Creek Swamp and KHC assemblages do not support the hypothesis of late survival of sthenurines on KI and indicates that further investigation of Seton Rockshelter is required.

Bettongia anhydra

While not directly related to the main topic of this thesis, chapter 3 dealt with a critical aspect of palaeontology, the importance of precision in fossil identification. Taxonomic revision of Australia's mammals has found several early species descriptions to be synonymous (e. g., *P. minnie* and *P. australis*). Whilst many of the synonymised forms were genuinely conspecific, morphologically similar species may not have been differentiated, particularly if they were poorly sampled and driven to extinction soon after Europeans colonised Australia. As species recognition is fundamental to biodiversity management it is important that species be rigorously examined before being synonymised to avoid taxonomic underrepresentation.

I examined material of all available species of *Bettongia* specimens from both the South and Western Australian Museums to develop my diagnostic expertise. In the process I observed that the holotype of *Bettongia penicillata anhydra*, collected from Lake Mackay in the Northern Territory (Finlayson 1957), which Wakefield (1967) synonymised with *B. lesueur*, was morphologically distinct from all other bettongs. Additional specimens from Holocene aged Western Australian cave accumulations shared markedly similar craniodental morphology to the Lake Mackay specimen, and confirm that it is sufficiently distinct from all other bettongs to warrant separation at the specific level as *B. anhydra*. This separation is also supported by preliminary ancient DNA results (M. Bunce and D. Haoucher pers. comm.) that will be included in the manuscript prior to publication.

Bettongs (along with potoroos and peramelids) excavate much of their food and in doing so perform valuable eco-services that improve soil structure and water infiltration and retention (Claridge *et al*. 2007). They also play a vital role in seed and fungal spore dispersal, which facilitates symbiotic relationships between fungi and numerous vascular plants (particularly *Eucalyptus* spp.) that are essential for plant recruitment and vegetation succession. Consequently, the near total loss of these ground-foraging mammals from the Australian landscape has far reaching ecological implications ranging from cessation of soil development and erosion to changes in vegetation structure and species distribution leading to habitat loss.

In addition to two species of bettong (*B. lesueur* and *B. penicillata*) the Late Quaternary mammal fauna of KI also included four other ground-foraging mammals, namely *Isoodon obesulus*, *Perameles bougainville*, *Potorous tridactylus* and *Potorous platyops*. With the exception of *I. obesulus*, all have been extirpated from KI or are extinct. *Bettongia lesueur* and *P. tridactylus* disappeared from the KHC fossil record more than 20 kyr ago but *B. lesueur* was present in the Seton assemblage until about 10 kyr ago. Extirpations of the remaining species are associated with European colonisation.

Pre-European mammals of the southern tip of Eyre Peninsula

The pre-European non-volant mammal fauna of the southern tip of Eyre Peninsula was investigated to assess similarities with the Holocene fauna of KI. The southern tip of Eyre Peninsula is a virtual island bound in the south by the Southern ocean and the north by aridity. Kangaroo Island and southern Eyre Peninsula share several non-volant mammal species in common (see Chapter 4). However, the mammal fauna of southern Eyre Peninsula includes several xeric adapted species that are not found on KI. This mirrors annual precipitation, of which southern Eyre Peninsula and western KI receive about 500 mm and 900 mm respectively (Schwerdtfeger 1985; Robinson and Armstrong 1999). The most remarkable feature of Eyre Peninsula's fauna is just how few native mammals have persisted beyond European settlement. This probably reflects the impacts that landscape modification and introduction of exotic species, particularly foxes and rabbits, which are absent from KI, have had on southern Eyre Peninsula's mammal communities.

Pre-European mammals of Yorke Peninsula.

The non-volant late Holocene mammal fauna of Yorke Peninsula was also analysed to investigate its similarity with the late Holocene fauna of KI. Like Eyre Peninsula, Yorke Peninsula is also a virtual island bound in the south by the Southern Ocean and the north by aridity. As the sea is shallowest between Yorke Peninsula and KI, Yorke Peninsula was probably the last part of the mainland to be separated from KI by rising seas. Consequently, it was hypothesised that the mammal fauna of Yorke Peninsula, and to a lesser extent Eyre Peninsula, would be quite similar. Yorke Peninsula has retained seven native non-volant mammals, an improvement over Eyre Peninsula, but still significantly reduced compared with its late Holocene fauna (30 species; see Chapter 5).

Radiocarbon dating showed that numerous small mammals still occurred on southern Yorke Peninsula after European settlement. Therefore, it is likely that Europeans were largely responsible for massive historical biodiversity loss, either through landscape modification or the introduction of exotic species. The pre-European fauna of Yorke Peninsula had a strong affinity with the pre-European fauna of southwestern Eyre Peninsula suggesting that prior to Holocene sea level rise mammal populations were likely continuous between the peninsulas and across the intervening lower-lying area that is now Spencer Gulf. Given that Yorke Peninsula was KI’s last connection to the mainland, mammals may have migrated between the two areas up until they were separated by sea water.

Chronology, stratigraphy and geochemistry of Kelly Hill Cave

This chapter investigated the chronology, sedimentology, geochemistry and source of sediments that fill KHC. The KHC infill sediment was excavated in 15 layers that were later concatenated into 7 units. AMS radiocarbon and U–Th dating of bone and speleothem respectively demonstrate that with the exception of unit 2 (layer 10) which has been reworked, over half of the strata excavated from KHC were fundamentally *in situ*. This interpretation is further supported by sedimentary microstructures observed in petrographic slides. Due to the absence of charcoal and speleothem and poor bone collagen preservation units 4–7 are yet to be dated. Optically Stimulated Luminescence samples collected from the KHC sediment sequence are currently being processed but ages are not yet available. However, associated *in situ* left and right dentaries of ‘*Procoptodon*’ *gilli* were found in unit seven along with a specimen of ‘*P.*’ *browneorum*. These species also occurred in the Seton and Black Creek Swamp assemblages. The youngest specimens recovered from the Black Creek Swamp assemblage have been dated at 45 kyr (Wells *et al*. 2006) and unlike Seton Rockshelter, remains of these species are yet to be retrieved from KHC strata dated at ≤20 kyr. Therefore, unit 7 has been tentatively ascribed a minimum age of 45 kyr, which in turn suggests that units 6–4 accumulated between 45 and 20 kyr ago. Thus, the sequence spans from the late Pleistocene to the middle Holocene and includes the LGM. Most of the sediments excavated were light to dark brown, fine grained and broadly classifiable as silty sands. However, petrography showed that about 50% of unit 6 (layer14) was made up of coarse-silt-sized clay pellets typical of sediment deflated from the surface of playa lakes which must have occurred on the continental-shelf southwest of KI during the Late Pleistocene. Geochemical analyses indicated that the silts and fine sands were derived from local parent sediments that were blown into the cave. This interpretation is further support by the occurrence of relic clay cutans on quartz grains which indicate that much of the cave sediments have been reworked from a developed soil and transported only a short distance before being deposited in KHC. Palaeoenvironmental interpretation of the KHC sedimentary sequence correlates well with environmental conditions deduced in other studies (e.g. Gingele *et al*. 2007) with the exception that Holocene-aged sediments suggest greater vegetation cover and higher precipitation on KI compared with mainland eastern Australia. These data provide a strong foundation for the following palaeontological analysis.

Faunal responses to isolation and environmental change

Following sedimentological and chronological analysis, the 15 layers excavated from KHC were grouped into seven units based on sedimentary and chronological similarity. As unit 1 was quite thick (60–75 cm) it was divided into three subunits based on age to better assess faunal change. The ecological structure of the KHC fossil assemblage changed dramatically over the last 40 kyr. The relative abundance of several heath species declined from the late Pleistocene into the Holocene, arid-zone species peaked around the LGM and the relative abundance of mallee woodland species increased during the Holocene. Despite dramatic changes in relative abundances only three species (*P. gunnii*, *B. lesueur* and *P. tridactylus*) were extirpated during the LGM suggesting that the majority of KI's mammal species were quite resilient to climate change. The species that disappeared during the LGM only ever occurred in low abundance and *B. lesueur*, an arid zone specialist (Claridge *et al*. 2007), occurred in the Seton Rockshelter until around 10 kyr (see chapter 2). Therefore, stochasticity may best explain the disappearance of these species from the KHC sequence. Faunal changes observed in the KHC sequence appear to have slightly preceded known climatic change. However, given its close proximity to the coast during the LGM and semi-continuous Southern Hemisphere westerly winds (Shulmeister *et al*. 2004; De Deckker *et al*. 2012) blowing from over the Southern Ocean, KI probably experienced more maritime conditions than expected across southern Australia during the LGM (G. Hope *et al*. 1977; Forbes *et al*. 2010). Evidence for wetter than expected LGM conditions are further supported by the discovery of late Pleistocene wetland in the Flinders Ranges (Williams *et al*. 2001).

The observed pattern of species loss after KI was isolated by sea-level rise appears to conform to predictions made by the theory of island biogeography. Comparison between fauna recorded in the youngest unit from KHC (6.8 kyr) and the oldest layer of Cape Du Couedic Rockshelter (>6.3 kyr) suggests that several mammals were extirpated soon after KI was isolated from the mainland by rising sea level. Species diversity appeared stable for the remainder of the Cape Du Couedic Rockshelter record which terminated around 4.7 kyr. The next youngest known faunal record, a European archaeological assemblage, has been radiocarbon dated to around 0.2 kyr old. In the large intervening time gap two species disappeared. Finally, following European colonization, the rate of mammal diversity loss accelerated once again with the extirpation of a further six species. The elevated rate of historical diversity loss is probably due to vegetation/habitat destruction and the introduction of cats, pigs, black rats and house mice as well as species exploitation by European fur trappers.

Potential for late-surviving megafauna

The Seton Rockshelter assemblage included the remains of megafauna (‘*P.*’ *gilli* and ‘*P.*’ *browneorum*) that appear to be less than 20 kyr old, suggesting that they survived on KI some 20–25 kyr later than anywhere else in Australia. 20 kyr ago KI was connected to the mainland and LGM climatic conditions were in effect. However, due to its proximity to the ocean and the occurrence of semi-continuous westerlies (Shulmeister *et al.* 2004), the colder, drier conditions typical of the LGM were probably ameliorated on KI. Local maritime conditions would have elevated local relative humidity and may have increased precipitation. This may explain why two species of short faced kangaroo apparently survived without being physically isolated from extinction risk factors. However, these species also occurred in the Black Creek Swamp and KHC assemblages. The youngest specimens recovered from the Black Creek Swamp assemblage have been dated at 45 kyr (Wells *et al*. 2006) and megafauna does not occur in KHC strata dated at 20 kyr. Therefore, evidence from the Black Creek Swamp and KHC assemblages do not support evidence of the late survival of megafauna suggested by the Seton assemblage. It appears that the only way to resolve the age of megafauna found in the Seton Rockshelter is to re-excavate the site in the hope of uncovering additional specimens then applying multiple cutting-edge chronological techniques to fresh bone, charcoal and quartz to seek an age consensus.

Evolution of Kangaroo Island's fauna

During ice ages exposure of the continental-shelf connected KI with four mainland bioregions, namely Southern Eyre Peninsula, Southern Yorke Peninsula, Fleurieu Peninsula and the Murray Mallee bioregion, each of which may have contributed to the Quaternary fauna of KI. Thirteen of the species found in the late Holocene non-volant mammal fauna of KI were ubiquitous to each region, 18 species (48.6%) were shared between KI and southern Eyre Peninsula, 20 species (54.1%) were shared between KI and Yorke Peninsula, 19 species (51.4%) were shared between KI and Fleurieu Peninsula (though due to the rarity of Holocene fossil assemblages on Fleurieu Peninsula species richness is probably underestimated) and finally, 33 species (89.1%) were shared between KI and the Murray Mallee bioregion.

Prior to Holocene sea level rise mammal populations were probably continuous between Eyre and Yorke Peninsulas and the intervening lower-lying area now occupied by Spencer Gulf. It was hypothesised that many of the mammal species found on KI would have mingled with those of the Eyre, Yorke and Fleurieu Peninsulas in a similar manner. The species richness of Late Holocene mammal assemblages from Eyre and Yorke Peninsulas are comparable (McDowell and Medlin 2010; McDowell *et al*. 2012) but each lack some of the more mesic-adapted species that occur on KI, namely *D. maculatus*, *D. viverrinus*, *Acrobates pygmaeus*, *Cercartetus lepidus*, *Mastacomys fuscus*, *P. apodemoides* and *Rattus lutreolus*. Instead they include more xeric-adapted equivalent species such as *D. geoffroii*, *Dasycercus* sp. indet., *Parantechinus apicalis*, *Phascogale calura*, *Sminthopsis psammophila*, *Leporillus apicalis* and *Pseudomys bolami*.

Similarities between Late Holocene faunas suggest that much of KI's non-volant mammal assemblage has been derived from South Australia's Murray Mallee bioregion. During the LGM the Palaeo-River Murray ran out over the Lacepede Shelf and flowed almost parallel to and within 50 km south of much of the southern coast of KI (Gingele *et al*. 2004; Hill *et al*. 2009; Schmidt *et al*. 2010). Mammals living in the Murray Mallee during the Holocene appear to have followed the Palaeo-River Murray out onto the Lacepede Shelf then up onto KI. Mammals that inhabited Eyre and Yorke Peninsulas may also have migrated to or from KI but do not appear to have made significant contributions to KI's non-volant mammal assemblage.

Potential for conservation biology

Late Holocene fossils demonstrate that prior to European settlement Yorke Peninsula, Eyre Peninsula and KI each supported diverse non-volant mammal assemblages. However, European land management practices, habitat modification and destruction and the introduction of exotic predators and competitors have decimated mainland native mammal communities. Today, Eyre and Yorke Peninsulas support four and seven native mammals respectively. KI has retained a much higher proportion (13 species) of its late Holocene fauna demonstrating that isolation resulting in the exclusion of rabbits and foxes can be beneficial to mammal communities. Combined with the retention of extensive tracts of near pristine native vegetation, KI would make an excellent refuge for a number of threatened mammals.

The Department for Environment and Heritage (DEH; now Department of Environment, Water and Natural Resources) are conducting reintroduction programs to re-establish mainland Tammar wallabies (*Macropus eugenii eugenii*) to Innes National Park, Yorke Peninsula (DEH 2004a) and Brush-tailed Bettongs (*Bettongia penicillata ogilbyi*) in Lincoln National Park, Eyre Peninsula (DEH 2004b). Extensive fox-baiting and rabbit control has been essential to help establish populations of both reintroduced species. As foxes and rabbits do not occur on KI and near pristine native habitat abounds, it may be less challenging to re-establish native species on KI than on the mainland.

The fossil record investigated here shows the potential for reintroduction of numerous threatened native mammals to KI has great potential for the successful re-establishment of threatened native species. Feral cats are a serious management issue on KI, but Dickman (1996) states that “cats have been present in Tasmania, on Kangaroo Island and in the northern parts of Australia for at least as long as anywhere else yet these places have retained virtually the full complement of their original fauna.” Given the findings of chapter 7, this statement is not strictly accurate (at least in the case of KI), though it does imply long term cohabitation of cats and Dasyurids in Tasmania and suggests that *D. maculatus* and *S. harrisii* could compete with cats if re-established on KI. They may even suppress the population density of feral cats, subsequently increase the chances of success for the reintroduction of other species. The fossil record indicates that *Phascogale tapoatafa*, *Acrobates pygmaeus*, *Cercartetus nanus*, *B. lesueur*, *B. penicillata*, *Onychogalea fraenata* and *Pseudomys occidentalis* once occupied KI. Of these, the latter four species have suffered the greatest range contractions (see Van Dyck and Strahan 2008) and may benefit most from reintroduction. The genetic source of reintroduction stock and number of individuals released are contentious subjects but ancient DNA analyses may help to identify regional genetic variations and whether different genetic variants should be preserved or interbred (e. g., Soltis *et al*. 1999). However, some of the species identified (e. g., *P. occidentalis* and *O. fraenata*) have suffered enormous range reductions while others (e. g., *B. lesueur*) presently exist only on small islands with limited carrying capacity. The establishment of new populations of these threatened species on KI using stock from all existing gene pools would provide some insurance against their extinction.

Significance of study

Kangaroo Island is the only land-bridge island on Earth known to have near complete vertebrate, vegetative and associated environmental records that span most of the Late Quaternary. This research examines part of that record from the late Pleistocene through to the Holocene, and is the first attempt to use palaeontological data (supported by other climate proxies) to track the actual effects that island isolation has had on a non-volant mammal assemblage. It substantially builds on our understanding of how the modern mammal fauna of KI developed; demonstrating that it has probably been derived from South Australia's Murray Mallee bioregion and may represent an extension of that bioregion during glacial periods.

The results of this study show that before being isolated from the mainland by rising Holocene sea-levels, KI possessed a rich and diverse continental-like mammal fauna. However, after isolation the mammal assemblage suffered a rapid extinction event, probably caused by elevated selection pressures resulting from isolation. This confirms predictions made by the theory of island biogeography, which have previously been supported by short-term studies of artificial islands only.

CONCLUSIONS

The effects of Late Pleistocene climate change on the mammal fauna of KI appear to have been minimal. Though the relative proportions of species abundance changed dramatically, few species were driven to extinction and those that disappeared were present sporadically only suggesting that their disappearance may be best explained by stochasticity. These findings bolster an increasing opinion that Australia's native fauna is quite resilient to climate change given the opportunity to shift with their preferred habitat, the loss of which appears to have a much more dramatic impact.

The effects of isolation on the fauna of KI were much more dramatic and negative. As predicted by the Equilibrium Theory of Island Biogeography, several species were extirpated soon after KI was isolated from the mainland. However, the prediction that extinction should impact the most resource demanding species earliest does not appear to have been met for all species.

This study provides baseline information to conservation, natural resource and landscape managers for the southern tip of Eyre Peninsula, Yorke Peninsula and Kangaroo Island and indicates that the extirpation of terrestrial mammals has largely resulted from European land management practices and the introduction of exotic predators and competitors. This had devastating effects on the terrestrial mammals of the Eyre and Yorke Peninsulas and only a few native mammals remain in those regions. Kangaroo Island has fared somewhat better, probably due to the absence of foxes and rabbits and the preservation of large tracts of unmodified native vegetation, which makes KI an excellent location for future species introduction and translocation programs.

Data from Seton Rockshelter suggested high potential for late-surviving megafauna to have occurred on KI. Radiocarbon dating of bone established that shelters strata had not been reworked. Fragmentation of the megafauna specimens, previously suggested as evidence of reworking was found to be consistent with all other specimens and the accumulation agent. However, attempts to direct date a sthenurine tooth fragment were unsuccessful. The same two sthenurine species that occur in Seton Rockshelter also occur in the Black Creek Swamp and KHC assemblages but appear to be aged between 40 and 50 kyr old. Re-excavation of the Seton site and application of improved dating techniques may be the only way to resolve this question.

If the isolation-induced extinction rates observed in the fossil record of KI are considered an analogue for predicting the long-term impacts of anthropogenic habitat fragmentation, the future of Australia’s remaining terrestrial mammals does not look bright. However, the rate of extirpation observed in the KHC assemblage was not alleviated by immigration, highlighting the importance of meta-populations and the preservation of native fauna on private property outside of the reserve system. Therefore, it is imperative that wilderness areas and biodiversity corridors be preserved wherever they exist to allow species to move with their habitat and mitigate the effects of climate change.

Future directions

This research provides a good understanding of how the modern fauna of KI developed, identifying both the biogeographic source of KI's mammal assemblage and the effect that isolation has had to mould the mammal community that persisted on KI when colonised by Europeans. However, the absence of datable bone, charcoal and speleothem from units 4–7 of the KHC sequence highlights the need for optically stimulated luminescence dates to better assess the timing of shifts in species abundance and the age of *in situ* sthenurine kangaroos recovered from unit 7. At least 1.5 m of unexcavated sediment exists beneath the current floor of the KHC excavation, promising an extended late Pleistocene record that may shed light on the fauna and palaeoenvironment of KI during that period. Additional mid- and late-Holocene aged palaeontological assemblages must also be located and investigated to fill knowledge gaps and confirm changes in fauna that have been deduced from existing archaeological assemblages. In addition, the relationship between the fauna of KI and the Murray Mallee should be further investigated. Finally, the study should be broadened by collaborating with other researchers to include analysis of amphibians, reptiles, birds, pollen, ancient mammal and plant DNA, body size change and fire history.

APPENDIX 1 – Charactering agents of accumulation

Pitfall traps

Pitfall trapping produces death assemblages that demonstrate a catastrophic age–frequency profile in which all age classes in a population are represented (Klein and Cruz-Uribe 1984; Wells *et al*. 1984; Wang and Martin 1993; Kos 2003). A diverse terrestrial fauna of diverse body sizes are expected due to indiscriminate nature of the trapping mechanism (Andrews 1990; Baird 1991). The expected breakage pattern of pitfall trapped animal bones include, a lack of fracturing or spiral and/or greenstick fracturing typical of fresh bone breaks (Bonnichsen 1973; Bonnichsen and Will 1980; Morlan 1980; Morlan 1983; Kos 2003; Reed 2006). In Australia, pitfall accumulations appear to be dominated by kangaroos. This may be due to their dominance of palaeocommunities, but Reed (2003; 2006) attributes it to their saltatory mode of locomotion which increases their susceptibility to pitfalls.

Mammalian Carnivores

Several authors (Douglas *et al*. 1966; Lundelius 1966; Hope 1973; Hope *et al*. 1977; Andrews and Nesbit Evans 1983; Baird 1991; Walshe 1994; 2000) have stated that the identification of a fossil assemblage as a mammalian carnivore den rests on three associations: 1) The presence of the osteological remains of the carnivore itself are present in the assemblage; 2) The presence of coprolites which contain the osteological remains of prey and can therefore be attributed to a carnivore; and 3) The presence of the osteological remains of prey animals whose collection can be attributed to a carnivore based on their size and condition eg: the degree of breakage, the presence of tooth marks. *Dasyurus maculatus*, *D. viverrinus* and *Sarcophilus harrisii* are the only native mammalian carnivores reported from Kangaroo Island and will be discussed below.

Dasyurus viverrinus

The Eastern Quoll has been recorded in a variety of habitats including dry sclerophyll forest, scrub, heathland and cultivated land (Godsell 1998; Jones 2008a). The species is described as a crepuscular nocturnal predator that can climb extremely well (Walton and Richardson 1988). *Dasyurus viverrinus* is an unselective opportunistic feeder that will consume a range of prey species from insects to small birds and mammals, and also scavenges large mammal carcasses (Green 1967; Baird 1991; Godsell 1998; Jones 2008a). Godsell (1998) and Blackhall (1980) found that Eastern Quolls subsist largely on a diet of insects, grubs, grasses and berries (which made up 55-84% of the food items recovered from scats) and that even though they are accomplished climbers, they predominantly fed on the ground. Blackhall (1980) noted that insect larvae constitute the bulk of this species diet at all times, and that small mammals such as house mice were apparently uncommon in the study area or were not favoured as food.

Eastern Quolls kill their prey by pouncing and pinning it with the forelegs then delivering a puncturing or crushing bite to the skull or upper neck which severs the spinal cord near its junction with the skull. Once it has achieved a bite to the head of its prey the Eastern Quoll employs a head shake, to enhance penetration of the canines and increase the effectiveness of the bite (Jones 1997). When attacking larger or defensive prey such as native rats, the quoll will aim for the head first (Pellis and Nelson 1984; Pellis and Officer 1987). Several historical accounts report that Eastern Quolls may drag the carcass of their prey to a lair in order to feed in safety (Blackhall 1980).

Lundelius (1966) conducted feeding tests on *D. maculatus* and *D. geoffroii*, in order to determine how quolls modified prey bones. He reported that test prey (white rats) were completely ingested and that bones passed in scats were highly fragmented. Lundelius (1966) also noted little difference in the size or shape of the faeces collected from the two species. Walshe (1994) estimated that the largest visible bone fragment present in the photographs supplied in Lundelius (1966) was approximately 10mm in length. Lundelius (1966) noted that there is a slight tendency for the smaller carnivore (*D. geoffroii*) to break up bone into smaller fragments, though this would probably be undetectable in a fossil assemblage.

Dasyurus maculatus

The tiger quoll (also known as the spotted-tailed quoll) is a medium-sized, moderately arboreal marsupial carnivore that occurs in a wide range of habitats, including wet scrub and coastal heathland, but is most reliant on wet forests. It eats a variety of prey species, including insects, crayfish, lizards, snakes, birds, domestic poultry, small mammals, platypus, rabbits, arboreal possums, macropods, and wombats, but tends to prey primarily on medium-sized (0.5–5 kg) arboreal mammals such as common brushtail (*Trichosurus vulpecula*) and ringtail (*Pseudocheirus peregrinus*) possums (Green and Scarborough 1990; Rounsevell *et al*. 1991; Baird 1991; Belcher 1995; Jones and Barmuta 1998; Jones *et al*. 2001; Belcher *et al*. 2007). However, rather than defecating in its den this carnivore favours latrine sites, often located on prominent high points (Jones *et al*. 2001; Belcher *et al*. 2007; Belcher *et al*. 2008), and so is unlikely to contribute to fossil accumulations.

Sarcophilus harrisii

Although present in all major habitat types in Tasmania, the Tasmanian Devil most commonly occurs in dry sclerophyll forest and coastal woodland, especially where interspersed with open grassland (Jones 2008b). Like the Eastern Quoll, this species has been describes as a crepuscular nocturnal predator (Walton and Richardson 1988).

Devils are predominantly scavengers and their dependence on carrion results in a highly diverse diet (Marshall and Cosgrove 1990). The Devil's diet has been reported to consist of rats, pygmy, ringtail and brush-tailed possums, bandicoots, quolls, potoroos, reptiles, birds and insects (Guiler 1970; Taylor 1986). However, Marshall and Cosgrove (1990) and Jones (1997) indicate that devils rely mainly on a few species of larger mammals such as wallabies (*Macropus rufogriseus*) and wombats (*Vombatus ursinus*) for the bulk of their food.

Prey killing by wild devils has rarely been documented, probably due to their scavenging nature. However, observations suggest that the method employed to subdue large prey involves gaining a grip with the jaws somewhere on the anterior half of the body, adjusting the bite until a vulnerable area such as the chest, neck or head is gained then hanging on with a crushing bite until the prey succumbs (Jones 1997).

The characteristics of *Sarcophilus* accumulated material are severe crushing, fracturing and corrosion, presence of circular punctures, frayed fracture of element ends and a wide range of body sizes for the animals represented. The surface corrosion occurs through dissolution by stomach acid, resulting in the removal of the surface cortex and the exposure of the trabecular tissue (Douglas *et al.* 1966; Lundelius 1966; Marshall and Cosgrove 1990; Baird 1991). Marshall and Cosgrove (1990) outline the characteristics that can be used to identify devil scat bone in fossil assemblages. These include the overall condition of bone to be extremely fragmentary with greater than 75% of the fragment measuring less than 15mm; the remains of larger prey suffer the greatest damage whereas smaller elements and the remains of small prey are usually more complete; digestive erosion etches bone surfaces but is of little importance compared with the degree of damage caused by the chewing action.

It is important to note that deposits accumulated by humans are difficult to distinguish from those accumulated by devils (Baynes *et al.* 1976; Baird 1991; Walshe 1994). Baynes *et al.* (1976) reported that present day Western Desert Aborigines chew the bones of small animals, such as rabbits or goannas, into small pieces and swallow them with the meat and that large kangaroo, emu and goat bones are commonly cracked up, chewed and swallowed in quite large pieces.

Raptors (Avian Carnivores)

Both diurnal raptors and/or nocturnal raptors may have contributed to cave accumulations. Several raptors have been recorded on Kangaroo Island but only a few of these are known to inhabit caves. Several researchers (Raczynski and Ruprecht 1974; Dodson and Wexlar 1979; Morton and Martin 1979; Marshall 1986; Hoffman 1988; Rensberger and Krentz 1988; Andrews 1990; Kusmer 1990; Dickman *et al.* 1991; Andrews 1995; Denys *et al.* 1995) have investigated various processes that a diverse range of raptors employ to capture their prey and to modify and accumulate their osteological remains. These studies, combined with observation of modern raptors have yielded an understanding of the distinct ‘signatures’ that each species of raptor impresses upon the remains of the prey that they accumulate. Thus, researchers are able to identify the primary accumulating species in modern and fossil assemblages by analysing both the types of prey species concentrated, and the ways in which the bones have been modified.

Raczynski and Ruprecht (1974), Dodson and Wexlar (1979) and Marshall (1986) all agree that the three processes dictate the extent to which prey bones are modified by raptors.

They are:

1. The method by which prey is captured,
2. The mode of consumption or ingestion, and
3. The extent of chemical erosion during digestion

These three processes will be examined for each raptor discussed.

Diurnal Raptors

Approximately 20 species of falcons, eagles and hawks have been recorded in the South East of South Australia but none of them are known to inhabit caves.

Diurnal raptors live in a range of habitats, but most commonly nest in forest and woodland, and often hunt over woodland and grassland. Not surprisingly, assemblages accumulated by diurnal raptors consist of diurnal creatures, and tend to contain a high percentage of insects, birds and reptiles, and low percentages of mammals. Diurnal raptors cause extensive mechanical breakage during the process of prey procurement and ingestion, and, as can be seen in Table 1, diurnal raptors assemblages are typically characterised by bones and teeth that have been subjected to heavy digestive erosion (Andrews 1990; Dickman *et al*. 1991).

Table 1: Bone Digestion Characteristics for Avian Predators (after Andrews 1990)

Predator Type	Characteristics
barn owl (nocturnal)	digestion absent or minimal - molar 0-3%, incisor 8-13%
greater owls (nocturnal)	moderate digestion; molars 4-6%. Incisors 20-30%
greater/ small owls (nocturnal)	heavy digestion; molars 18-22%, incisors 50-70%
eagle/hawk (diurnal)	severe digestion; molars 50-70%, incisors 60-80%
henharrier/ buzzard (diurnal)	extreme digestion; molars 50-100%, incisors 100%

Nocturnal Raptors

Five species of owls have been recorded in the South East during European history and may also have existed on Kangaroo Island. Of these, three are members of the genus Strigidae and remaining two are members of the genus Tytonidae (Parker and Reid 1983). Three species, *Tyto alba*, *Tyto novaehollandiae* and *Ninox novaeseelandiae*, are known to roost in caves. Lundelius (1966) and Andrews (1990) state that nocturnal raptor accumulations display the following characteristics:

1. Long bones are intact; skulls are either intact or disarticulated into their component bones; mandibles are not highly fragmented; and there is little or no evidence of bones or teeth erosion.
2. There is a bias towards small mammals, particularly murids and small dasyurids; species larger than 200g are predominantly represented by juveniles and sub-adults.
3. Evidence for collection by diurnal raptors such as heavy digestive erosion of bones and teeth is absent.

Family Strigidae

The three strigid owls that have been recorded in the South East of South Australia include *Ninox strenua*, *Ninox connivens* and *Ninox. novaeseelandiae*. Strigid owls usually roost in trees. *N. strenua* and *N. connivens* characteristically feed primarily on large arboreal mammals such as ringtail and brushtail possums (Parker and Reid 1983; Hollands 1991; Lavazanian *et al*. 1994; Pavey *et al*. 1994; Pavey 1995). In contrast, *N. novaeseelandiae*, while known to roost in caves, is a much smaller animal that feeds mainly on insects (Hollands 1991).

Family Tytonidae

Two species of tytonid owls have been recorded in the South East, both of which are known to roost in caves. As previously mentioned, these species are *Tyto alba*, the Barn Owl, and *Tyto novaehollandiae,* the Masked Owl.

Tyto alba

The Barn Owl has been given its name for its habit of roosting in the rafters of farm buildings throughout the Old World and America. It is probably the most widespread of all land-based birds, inhabiting all of the continents except Antarctica (Hollands 1991). This species is highly dependent on the availability of adequate food resources, and as a result is often nomadic, relying on rodent plagues to boost their numbers. However, in areas that support abundant prey Barn Owls will remain faithful to a single area and even a single breeding site for generations (Morton and Martin 1979; Hollands 1991). Barn Owls inhabit woodland, grassland and forests, and nest in both trees and caves (Simpson and Day 1999). Hollands (1991) observes that “Barn Owls are specialist hunters of small ground mammals and the overwhelming majority of their food consisting of small rodents”. Barn Owls predominantly prey on nocturnal mammals weighing less than 200g, but their prey may also include juvenile larger mammals (eg. bandicoots and bettongs). As this species becomes active before dusk its diet may also include frogs, lizards, small birds and to a lesser extent insects (Morton 1975; Morton *et al*. 1977; Baynes 1979; Morton and Martin 1979; Marshall 1986; Hollands 1991).

Barn Owls hunt their prey by watching and listening from a vantage point near the ground such as a low tree limb or fencepost, or by flying slowly close over the ground in a quartering pattern. The characteristic heart shaped face disc acts like a reflector, collecting sound and channelling it to the animals ears which are made asymmetrical by flaps of skin that act as ear trumpets. This causes sound to reach the two ears at slightly different times from different angles, allowing much greater auditory acuity, and therefore, pinpoint accuracy. Barn Owls capture their prey by dropping onto them from above, grasping with extended talons and delivering a killing bite with the beak (Bunn *et al*. 1982; Hollands 1991).

Barn owls cause very little modification to the bones of their prey. Several authors (e. g., Kusmer 1990; Racznski and Ruprecht 1974) report minimal mechanical bone breakage during prey capture. Similarly, bone breakage during ingestion is limited, probably because Barn Owls concentrate on small prey that is typically swallowed whole (Kusmer 1990). As suggested by Table 1, digestive erosion of the osteological remains of barn owl prey is almost totally absent.

Tyto novaehollandiae

Known as the Masked Owl, *T. novaehollandiae* is larger than the Barn Owl and much less common. It is a reasonably sedentary species with breeding pairs occupying large ranges and several roosts on a rotational basis (Marshall 1986). Masked Owls usually nest and roost in dense Eucalyptus forest (as well as caves) but prefer to hunt over open woodland, forest margins, bushland and cleared grassy areas (Marshall 1986; Hollands 1991; Kavanagh and Murray 1996; Simpson and Day 1999).

Masked Owls have been observed to prey upon both terrestrial and arboreal mammals although terrestrial prey predominates. Arboreal prey includes *P. breviceps*, *P. peregrinus* and *T. vulpecula* and terrestrial prey consists predominantly of large and small dasyurids and rodents (Hollands 1991; Kavanagh and Murray 1996; Morris *et al*. 1997). Mooney (1993) reported that *T. novaehollandiae* concentrates on a range of prey weighing between 200 and 600g, and rarely preys upon mammals weighing less than 200g. Further, Mooney (1993) believed that large, difficult to procure prey was a more important component of the Masked Owls diet in prehistoric times than in historic times.

Masked Owls hunt prey both on the ground and in the trees in a similar fashion to the Barn Owl. However, the majority of its prey is obtained by waiting on a perch rather than on the wing. Masked Owls capture their prey with extended talons and usually dismember and ingest it on the spot as well as at the perch (Marshall 1986).

Due to their rarity, little has been documented of the prey-bone modifications that typify Masked Owl deposits. Marshall (1986) suggested that Masked Owls, taking larger prey, may inflict more mechanical damage during prey procurement and ingestion, especially with prey that must be dismembered before ingestion, but called for further experimental investigation into the taphonomy of Masked Owl deposits. It is thought that the acidity of *T. novaehollandiae* stomach fluid is comparable to that of *T. alba*. Therefore, little digestive erosion should occur.

APPENDIX 2 – Dating Methods and Applications

A robust chronology is fundamental to the study of Quaternary palaeontology and palaeoecology (Ayliffe *et al*. 2008; Forbes *et al*. 2009; Magee *et al*. 2009). A number of dating methods can be applied to Quaternary research, include Radiocarbon, Uranium series, Thermo and Optically Stimulated Luminescence (TL and OSL respectively), Electron Spin Resonance (ESR) and Amino Acid Racemisation (AAR) dating. Each of these methods can be used to estimate the age of specific kinds of material, but the most appropriate method to apply is often dictated by the type of datable material available, the depositional circumstances and the expected age range of the deposit (Grun 2007; Jull 2007a).

Radiocarbon dating was developed in the late 1940's–early 1950's and relies on the natural decay of radioactive carbon (^{14}C) isotopes at a half-life rate of 5.73 kyr. This allows a practical dating range of 0–50 000 years. The method can be applied to any material that contains organic or inorganic carbon, which must be in equilibrium with atmospheric ^{14}C production (Burr 2007; Ramsey 2008). Radiocarbon dating initially done by counting beta partial emission from a solid source, but was later carried out using either liquid scintillation or gas proportional counting (Cook and van der Plicht 2007). Whilst these techniques are still used today, the development of accelerator mass spectrometry (AMS) has made it possible to accurately estimate the age of much smaller samples (Jull 2007b). Radiometric and AMS analysis for ^{14}C are fundamentally different. The former is accomplished by measuring the radiation produced by decay of ^{14}C atoms while the latter measures the number of ^{14}C atoms relative to the number of ^{12}C and/or ^{13}C atoms (Cook and van der Plicht 2007). Irrespective of the method employed, to ensure accurate dating it is important to measure only ^{14}C that was part of the organism when it died. To achieve this, samples are exposed to rigorous physical and chemical 'pre-treatment' processes that are designed to remove extraneous carbon that may be incorporated into the sample from the burial environment and isolate the fraction of the sample that is most suitable for dating (eg: cellulose from wood, and collagen from bone) (Hedges and Van Klinken 1992; Cook and van der Plicht 2007).

To facilitate interpretation, radiocarbon ages are calibrated into calendar years (Reimer and Reimer 2007; Scott 2007). Due to fluctuations in atmospheric ^{14}C during the last millennium it is difficult to calibrate young radiocarbon ages, so these are typically reported in radiocarbon years (Burr 2007; van der Plicht 2007). Due to difficulties in showing contemporaneity between charcoal and skeletal remains, it is preferable to estimate radiocarbon age using collagen isolated from bone. However, the intactness and purity of collagen is strongly dependent on the extent of diagenetic degradation, contamination and the extraction method. (van Klinken 1999). Dating bone from a known genus also allows the researcher to minimise error introduced form the embodied age of the specimen dated (Ramsey 2008).

Uranium series dating relies on the uranium decay series. Some of the radioactive decay pairs of uranium and its daughter isotopes can be used to measure time on various scales, depending on the radioactive pair chosen, providing a practical dating range of 1000–500 000 years (Ku 2000; Jull 2007a). This process has a wide variety of applications and can be used to date sediments, soil horizons, peat, bones, corals, and carbonates. However, it is susceptible to a number of sources of error and in cave environments is best applied to clean speleothems (Ayliffe and Veeh 1988; Schwarcz 1989; Moriarty *et al*. 2000).

TL and OSL and ESR are part of a family of techniques called 'Trapped Charge Dating' (Grun 2007). These methods are based on the time-dependent accumulation of free electrons in defects in the crystal lattice of minerals to provide an age-dependent signal (Hennig and Grun 1983; Grun 2007; Wintle 2007). Each technique differs in the instrumentation and physical processes that are used to measure the naturally accumulated dose (Grun 2007). Unlike most of the other dating methods, Trapped Charge Dating techniques do not provide the age of formation of the mineral grains to which they are applied. Instead, they determine the last point in time at which the grains were either heated or exposed to light. When applied to sedimentary grains, these techniques can help determine the time since the grains were last exposed to light, providing a depositional age (Wintle 2007). TL and OSL are capable of dating quartz and feldspar grains that were deposited between 100–10^6 years ago, while ESR is capable of dating quartz and tooth enamel between a few hundred years up to 2 million years (Grun 2007; Jull 2007a). The greatest advantage of ESR dating is that it is virtually non-destructive, and can be used to directly date tooth enamel. However, in some cases other techniques may be applied faster, cheaper and with greater reliability (Grun 2007).

Amino acids, the basic chemical units from which proteins are formed, can exist in two molecular isomers. In living materials, they usually occur only in one form (L-type), and after death they convert to the other form (D-type) (Wintle 2007). This process, known as racemisation, occurs over time until the two forms reach equilibrium. This technique can be used to date mollusc and bird egg shell aged between 10–10^6 years (Jull 2007a; Miller and Clarke 2007; Wintle 2007).

Recent studies (eg: Ayliffe *et al*. 2008; Magee *et al*. 2004; Turney *et al*. 2008; Darrénougué *et al*. 2009; Magee *et al*. 2009) have shown that the most reliable chronologies are achieved by applying several dating techniques to the same accumulation.

APPENDIX 3 – Climate Proxy Records

Stable Carbon Isotope Analyses

The ratio of stable carbon isotopes (C^{13}:C^{12}) can be used to address several geochemical and biochemical problems (Craig 1953). Mammal bone phosphate (Longinelli 1984; Luz *et al*. 1984; Luz and Kolodny 1985; Ayliffe and Chivas 1990) and land mollusc shells (Baroni *et al*. 2006; Prideaux *et al.* 2010) may also be used to determine palaeoclimatic conditions. As bone is constantly remodelled throughout an animal's life, carbon incorporated in aragonite land snail shells may offer a more accurate palaeoclimatic record. Land snails precipitate aragonitic shells that are in isotopic equilibrium with the bicarbonate pool of its body waters (Prideaux *et al.* 2010). Stable carbon isotope composition of respired CO_2 determines the $\delta^{13}C$ of the bicarbonate pool which appears to be determined by a variety of external environmental parameters (Goodfriend *et al*. 1989). Land snail shell carbon isotopes are thought to be related to snail diet (usually comprised of local vegetation with minor contributions from limestone substrates) making them a good indicator of environmental conditions including temperature (Francey 1983; Goodfriend and Hood 1983; Goodfriend *et al*. 1989; Prideaux *et al.* 2010). Analytical methods are described by Prideaux *et al.* (2010).

Stable Oxygen Isotope Analyses

Research on oxygen isotope ratios, pioneered by Emiliani (1955), has probably contributed most significantly to our understanding of global climate change. During ice ages, much of the water evaporated from oceans becomes locked in polar ice sheets. As water containing the lighter oxygen isotope (O^{16}) is preferentially evaporated (and locked in ice), oceans become enriched with the heavier oxygen isotope (O^{18}). Planktonic foraminifera use the oxygen in sea water to build their calcareous shells. Thus, oxygen isotope ratios measured from planktonic foraminifera that have been extracted from marine sediment cores or ice cores can provide oxygen isotope curves that outline the major features of the earth's glacial-interglacial fluctuations. A refined and detailed chronology of palaeoclimatic fluctuations has now been established from several continuous deep sea cores (Belperio 1995).

Oxygen isotope stages have been superimposed on these isotope curves with boundaries corresponding to periods of rapid isotope change in the palaeo-oceans. These boundaries have been dated using a combination of palaeomagnetic reversal stratigraphy and radiometric dating (Berggren *et al*. 1980; 1985) and correspond closely to periodicities of the Earths Milankovitch orbital parameters. Thus, oxygen isotope ratios provide a robust general record of palaeoclimatic fluctuations against which all other climate proxy records can be compared.

Mammal bone phosphate (Longinelli 1984; Luz *et al*. 1984; Luz and Kolodny 1985; Ayliffe and Chivas 1990) and land mollusc shells (Baroni *et al*. 2006; Prideaux *et al.* 2010) may also be used to determine palaeoclimatic conditions.The oxygen isotope compositions of the bone phosphate of some mammals are related to the oxygen isotope composition of meteoric water. Mammal-bone is well suited for palaeoclimatic reconstructions of terrestrial environments for a number of reasons (Ayliffe and Chivas 1990). Bone mineralisation is a process that is known to involve the enzyme adenosine triphosphate (ATP) (Leonard and Scullin 1969; Dahms and Boyer 1973; Faller and Elgavish 1984; Ayliffe and Chivas 1990). This enzyme promotes rapid exchange of $^{18}0$ between the precipitating bone phosphate and the water in body fluids that are intimately involved in this process (Leonard and Scullin 1969; Ayliffe and Chivas 1990).

However, bone phosphate is constantly remodelled resulting in a multi-year average record of an animal's diet. In contrast, tooth enamel carbonate, once formed, is not remodelled (Kohn *et al*. 1996; Fraser *et al*. 2008; Grimes *et al*. 2008). Several studies that use fossil teeth to provide Oxygen isotope records have been made (Kohn *et al*. 1996; Lindars *et al*. 2001; Vennemann *et al*. 2002; Passey and Cerling 2006; Bocherens and Drucker 2007; Fraser *et al*. 2008; Grimes *et al*. 2008). Lindars *et al*. (2001) and Grimes *et al*. (2003) developed a direct laser fluorination technique, with a new pretreatment procedure, to analyse the phosphate oxygen from the enamel of small mammal teeth (for example, rodents) for use in continental palaeoclimate reconstruction. Fraser *et al*. (2008) showed that while erratic, it is possible to obtain a δ^{18}O microprofile from wombat teeth, giving a record of changing δ^{18}O with time. Lee *et al.* (1999) investigated rodent exposure to heavy metal s through time using laser ablation to systematically sample along continuously growing rident incisors. Grimes *et al*. (2008) reviews the advantages and disadvantages of using small mammals as a source of δ^{18}O. They argued that before small mammals could be routinely used in the determination of $\delta^{18}O_{lw}$ values two key requirements had to be met. Firstly, it must be demonstrate that the majority of a small mammal's water intake came from the consumption of water, rather than from their food. Secondly, the enamel must not have been diagenetically altered. If these sampling methods could be combined it may be possible to obtain a δ^{18}O microprofiles from rodent incisors.

Dune Activity

Glacial periods are commonly associated with a dramatic fall in temperature and sea-level that results in an increase in continental margin (Belperio *et al.* 1995; Murray-Wallace 2002, 2007). As a result, dune activity in continental centres often increases. Dune activity phases in Australian deserts during the last glacial-interglacial cycle have been investigated by Wasson (1986; 1989), Belperio *et al.* (1995), Nanson *et al*. (1995), Maroulis *et al*. 2007; Fitzsimmons *et al*. 2007 and Murray-Wallace (2002, 2007). Coastal dune activity in Eastern Australia has been reviewed by Thom *et al*. (1994). Dune activity associated with the Last Glacial Maximum (LGM) in Australia's major dunefields occurred between 36kyr and 14kyr, beginning under periglacial conditions (Wasson 1986; 1989; Nanson *et al*. 1995). Wasson (1989) showed correlations between dune activity (in both Australia and New Zealand), periods of low global temperature and periods of high wind speeds for the last 150kyr. However, Hesse and McTainsh (1999) demonstrated that Southern Hemisphere mid-latitude winds were no stronger during the LGM than in the Holocene. They concluded that dune building during the LGM was the result of reduced vegetation cover caused by decreased evapotranspiration/precipitation ratios, though changes in the fire regime may have contributed. Lampert (1981) demonstrated that dune building also occurred on Kangaroo Island at this time.

Charcoal analysis (Fire history)

Charcoal analysis quantifies the accumulation of charred particles that have accumulated in sediments. Stratigraphic levels that contain abundant charcoal are interpreted as evidence of past fire events (Whitlock and Larsen 2001). Charcoal particle size can indicate fire frequency and temperature and may indicate arrival or departure of humans (Grayson 2001). Collection and analysis procedures are outlines in Whitlock and Larsen (2001), Burney and Burney (2003) and Couzens (2007). Pollen and charcoal data from the same strata can be used to examine the linkages among climate, vegetation, fire, and potentially human activities in the past (Whitlock and Larsen 2001).

Palynology and Palaeolimnology

Decreased evapotranspiration/precipitation ratios during the LGM are supported by Palaeolimnological research. Palaeo-lake levels have been investigated at Willandra Lakes (Bowler *et al.* 1976), Lake Keilambete (Bowler *et al.* 1976; Dodson 1974a) and the Hattah Lakes region (Kotsonis *et al*. 1999). Results obtained from these studies showed that in all of these lakes, the onset of dry conditions began approximately 38–36 kyr ago, under periglacial conditions. Palynological records have been extensively researched in the South East of South Australia (Dodson 1974b; 1975; 1977; Dodson and Wilson 1975) and Western Victoria (D'Costa and Kershaw 1995; D'Costa *et al*. 1989; Edeny *et al*. 1990; Harle *et al*. 1999), while Harle (1997) has reported the palynology of Marine Core E55-6, located offshore of the South Australia/Victoria border. The aforementioned studies all agree that about 50 000 years ago (Oxygen Isotope Stage 3), the vegetation of the south-eastern Australia changed from *Eucalyptus* forest with heath understorey to *Eucalyptus* woodland with heath and grass understorey. In isotope stage 2 (25–12 kyr) woodlands become more open with *Casuarina* and *Banksia* species becoming more prominent. During stage 1 (12–0 kyr), closed *Casuarina*/*Eucalyptus* woodlands predominated. These vegetation changes reflect the overall trend that south-eastern Australia was experiencing a drier and more seasonal climate during the Quaternary (Kershaw 1995; Kershaw *et al*. 1991).

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